

Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes

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Synopsis

The fifteen families recognized by Peters (1945, 1948) as comprising the orders Coraciiformes and Piciformes form the subject of this study, which is presented in four parts. The first summarizes available information on feeding behaviour from fieldwork and the literature. In the second part, which constitutes the main results of the investigation, a detailed account of the anatomy of jaws, tongue and neck is given.

Part three examines the anatomical findings from functional and evolutionary standpoints. Overall skull form is discussed in relation to diet, posture and requirements for vision. Kinetic coupling is achieved either via the postorbital ligament, or by modifications of the quadrate-mandible articulation (*Bucorvus* and *Megalaima*); factors affecting the degree and type of coupling are examined. Bony stops and other safety devices present in the kinetic apparatus are reviewed, and their effectiveness assessed. Functional properties of the desmognathous palate are examined; it is noted that this condition is present in large-billed forms, and in families which regularly beat prey against a perch. A distinctive form of pterygo-palatine articulation is present in the Indicatoridae and Picidae; the need for studies of its ontogeny is pointed out. The lower jaw lacks structural features permitting gape enlargement by bowing the mandibular rami, despite the large food items swallowed by many species; possible reasons for this are discussed. Maintenance of the quadrate-mandible articulation is analysed; a medial brace or a deepened medial quadrate condyle are compared as possible alternative forms of protection in groups consuming large or active animal prey.

M. adductor mandibulae externus is the most complex and variable jaw muscle. A detailed compari-

son of its components is made between the families studied here, and published descriptions for birds of other orders. On this basis, certain features (especially the postorbital lobe, narrow M.a.m.e. ventralis and laterally expanded M.a.m.e. caudalis) are considered primitive; the Phoeniculidae and Picidae show these features particularly well. Simpler architecture of this muscle is considered derived, but there are indications that its condition in most Coraciiformes and the Galbuloidea was derived independently from that seen in other Piciformes. The functional significance of complex vs. simple architecture of the muscle is discussed. *M. pseudotemporalis superficialis* has a mainly lateral origin in typical Coraciiformes and the Galbuloidea, although the whole muscle is much reduced in some groups, and occasionally absent in the Galbulidae. By contrast, a medial extension of origin is developed in typical Piciformes. *M. pseudotemporalis profundus* is generally parallel fibred, varying mainly in size. It is absent in many Alcedinidae as a consequence of changes in skull form. *M. pterygoideus dorsalis* is clearly divided into lateral and medial parts, except in the Upupidae, Phoeniculidae and *Ramphastos*. The functional significance of division, and the relative proportions of the two components are discussed. In several families, *M. pter.dors.lat.* has attachment to the maxillopalatine, permitting the muscle to exert force on the upper jaw directly, rather than through the palatal complex—a feature previously undescribed in birds. Bipinnate structure of *M. pter.dors.lat.* in several families may be related to small amplitude jaw movements or to isometric contraction. A slip attached directly to the skull base (retractor palatini) is present in the Upupidae, Phoeniculidae and Bucerotidae, derived from *M. pter.dors.med.* and *vent.med.* *M. pter.dors.med.* is divided into anterior and posterior portions in the Coraciidae and Leptosomatidae. *M. protractor* is much enlarged in the Upupidae, Phoeniculidae and Picidae. In the first two families, this is related to foraging by 'gaping', and is associated with a bulky *M. depressor*, but in the Picidae, enlargement is a consequence of the muscle's shock absorbing function during hammering, and *M. depressor* is of normal size.

The tongue is much reduced in the Alcedinidae, Upupidae, Phoeniculidae and Bucerotidae. This may be related to diet in the Alcedinidae, and to bill reinforcement in the Upupidae and Phoeniculidae. Brush tongues occur in several families, showing no obvious correlation with diet or feeding methods. The Picidae show reduction of the tongue itself, but great elongation of the basihyal and hyoid horns to form a probing organ capable of great extension, with a capacity for fine manipulation at the tip. Comparison with other families of typical Piciformes gives some insight into the evolution of this feature. Most Capitonidae, the Ramphastidae and the Indicatoridae possess an entoglossum of distinctive and unusual form.

M. ceratohyoideus is lacking in the Alcedinidae, Indicatoridae and Picidae. *M. stylohyoideus*, the main tongue retractor, is lost in the Bucerotidae, which rely largely on head jerking to propel food items backward to the oesophagus. It is also absent in the Coraciidae, Galbulidae and Bucconidae, where it is functionally replaced by a slip from *M. serpihyoideus*; in *Leptosomus*, both this slip and an *M. stylohyoideus* are present. *M. branchiomandibularis* ranges from very highly developed in the Picidae to virtually absent in the Alcedinidae. Its sites of origin vary extensively among the Coraciiformes, and may be related to the history of the sporadically distributed *M. genioglossus*. *M. ceratoglossus anterior* and *M. hypoglossus medialis* are best developed in the Meropidae and Galbulidae. *M. hypoglossus obliquus* is considerably elongated in the Upupidae, Phoeniculidae and typical Piciformes; contracting synergically with *M. ceratoglossus*, this imparts rigidity to the tongue/basihyal unit during forceful probing actions. Extreme development of this condition is seen in the Picidae, with some approach in the Indicatoridae. *M. tracheohyoideus* originates either on the clavicle (Coraciiformes and Galbuloidea) or on the sternum (typical Piciformes). In the Bucerotidae it originates on both: this may be the primitive condition from which the two alternatives are derived.

The cervical vertebrae show reduction or loss of fused ribs in the Bucerotidae and Picidae, and in the former, the first and second vertebrae are fused. A sub-vertebral canal is well developed in the Picidae; though enclosing the carotids, its primary function is probably to provide increased surface for attachment of the highly developed *M. longus colli ventralis*.

The evolution of neck muscle attachments is discussed; reduction in attachment sites is probably a derived state in most cases, but the possibility that increased numbers of attachments might evolve should perhaps not be discounted. *M. biventer cervicis* is strikingly enlarged in the Alcedinidae, presumably to maintain posture of the heavy head and bill; the Cerylinae and some Daceloninae possess a transverse aponeurosis between right and left muscles. The muscle is also enlarged in *Jynx* and *Indicator*, but in specialized excavators (Upupidae, Phoeniculidae, other Picidae) it is reduced. *M. splenius capitis* has additional origin on 3 in *Phoeniculus* and some Bucerotidae. *M. longus colli* is highly specialized in the Picidae, with short slips eliminated and long ones enlarged, enabling the neck to be held rigidly flexed during hammering. *M. complexus* is highly developed in the Alcedinidae, with origin as far back as 8 or 9 in some; the mechanics and adaptive significance of this are discussed.

M. rectus capitis lateralis is unusually small in the Galbuloidea, where its role may be partly taken over by *M. splenius capitis*.

In the fourth and final part of the paper, the principal features of feeding apparatus structure are summarized family by family, and their adaptive and taxonomic significance are discussed. The concluding section examines the picture of phylogeny which emerges for the assemblage as a whole. Three main phyletic lines are envisaged; the first consists of the first six Coraciiform families of Peters (1945) together with the Galbuloidea. This line is itself split between the Alcedinidae, Todidae, Momotidae and Meropidae on the one hand, and the Coraciidae, Leptosomatidae, Galbulidae and Bucconidae on the other. The Upupidae, Phoeniculidae and Bucerotidae are considered to represent a second major line, in which the first two families are more closely allied, while the third line consists of the four remaining Piciform families. Among these, the Indicatoridae and Picidae are closely allied, with *Jynx* occupying a somewhat uncertain position between the two. The Ramphastidae are considered directly derived from the Capitonidae. In the classification proposed on the basis of this phylogeny, the Brachypteraciinae and Jynginae are given family rank. The Ramphastidae are, for the present, retained as a family.

Introduction

The avian orders Coraciiformes and Piciformes, as defined by Peters (1945, 1948) comprise 15 families of mainly small to medium sized birds, remarkable for their morphological diversity. This diversity is nowhere more clearly shown than in the structure of the feeding apparatus, so that they form an ideal subject for studies of feeding adaptations and functional anatomy. Curiously, though, relatively scant attention has been paid to these matters, except in the case of the Picidae. Probably, this is because questions of pure taxonomy have always been uppermost, for although some alliance between the two orders has long been generally accepted, the interrelationships of their component groups have never been satisfactorily clarified. The study presented here has concentrated on the adaptive aspects hitherto neglected, but at the same time, has furnished extensive new evidence relating to the evolution and affinities of the various families.

A detailed historical review of the classification has been given by Sibley & Ahlquist (1972), and need not be repeated here. However, some resumé of the present state of knowledge is necessary, and can be conveniently grouped under the headings of three possible types of relationship.

1. Relationships between families within an order. More problems are presented by the Coraciiformes, which fall roughly into three groups. Most heterogeneous of these is that made up by the Alcedinidae, Todidae, Momotidae and Meropidae, which in most respects show only a loose affinity, but share a distinctive stapes form (Feduccia, 1977, 1980). The Coraciidae (including the Brachypteraciinae, treated as a family by some authors) seem fairly definitely allied to the Leptosomatidae (see Cracraft, 1971), but both appear rather distantly related to the preceding families. The Upupidae, Phoeniculidae and Bucerotidae are usually considered to be allied, but the connection between these three and the rest of the order seems less obvious.

Within the Piciformes, relationship between four of the families (Capitonidae, Indicatoridae, Ramphastidae and Picidae) seems fairly well established, but the position of the Galbuloidea (Galbulidae and Bucconidae) is more open to question (but see Steinbacher, 1937).

2. Relationships between Coraciiform and Piciform families. Sibley & Ahlquist (1972) have produced biochemical evidence for affinity between the Galbuloidea and Alcedinidae, and in view of the uncertain position of the former relative to the rest of the Piciformes, the possibility of a connection with the Coraciiformes must be taken seriously.

3. Relationships with other orders. Many such have been proposed in the past, but only three seem at present to merit further investigation. These are, the possible connections between the Indicatoridae and the Cuculiformes (Sibley & Ahlquist, 1972), between the Trogoniformes and the Coraciiformes (Sibley & Ahlquist, 1972; Feduccia, 1977) and

between the Piciformes and the Passeriformes. To keep this study within practical limits, only members of the Coraciiformes and Piciformes have been included. However, the findings presented here have some relevance to two of these suggested relationships, arguing strongly against any honeyguide—cuckoo connection (p. 433), but providing tentative support for associating the trogons with the Coraciiformes (p. 437).

The first two parts of this paper are factual, and the following two interpretative. A survey of available information on feeding behaviour is followed by the detailed descriptive anatomy which constitutes the main results of the investigation. In the third part, the anatomical systems studied are re-examined from a functional and evolutionary perspective, and in the final part, the families are reviewed in turn, considering both adaptive and taxonomic aspects. The concluding discussion deals with the principal taxonomic problems, and presents a phylogeny and classification based on the results of the study. The taxonomic nomenclature and classification used is that of Peters, but a problem exists in regard to the naming of structures. This manuscript was already largely complete when the *Nomina Anatomica Avium* (Baumel, *et al.*, 1979) appeared, and not all the anatomical names used were in agreement with it. The revision needed to achieve total agreement with the N.A.A. would have been a daunting proposition, but it is hoped that the lesser adjustment which has been adopted will suffice. This is to give the N.A.A. equivalent in brackets following all headings in Part 3 which use a superseded term.

Material examined

The anatomical specimens that were available for this investigation are mostly those listed by Blandamer & Burton (1979); the main addition to the orders studied since this list was published is a specimen of *Bombylonax breweri* (Meropidae) presented by Dr C. H. Fry. At least one specimen of every genus in the alcoholic collection has been dissected, and several species in the case of large genera such as *Halcyon*; skeletons of all available genera have also been examined. Four species absent from the collections of the British Museum (Natural History) were loaned by the American Museum of Natural History; these were *Galbula tombacea*, *Brachygalba lugubris* (Galbulidae); *Nystalus maculatus* and *Hypnelus bicinctus* (Bucconidae).

Birds of several other orders have been dissected to check specific points, and these are noted in the text.

Abbreviations

Jaw muscles, figs 7–24

amec	M. adductor mandibulae externus caudalis
amer	M. adductor mandibulae externus rostralis
amerl	M. adductor mandibulae externus rostralis lateralis
amerm	M. adductor mandibulae externus rostralis medialis
amerp	M. adductor mandibulae externus rostralis, postorbital slip
amert	M. adductor mandibulae externus rostralis temporalis
amev	M. adductor mandibulae externus ventralis
amevc	shared fibres of M. adductor mandibulae externus ventralis and caudalis
ap	M. adductor posterior (N.A.A.: M. adductor mandibulae caudalis)
dm	M. depressor mandibulae
pr	M. protractor pterygoidei et quadrati
pr1	M. protractor, part 1
pr2	M. protractor, part 2
psp	M. pseudotemporalis profundus
pss	M. pseudotemporalis superficialis
pssl	M. pseudotemporalis superficialis, lateral part
pssm	M. pseudotemporalis superficialis, medial part

ptd	M. pterygoideus dorsalis
ptdl	M. pterygoideus dorsalis lateralis
ptdm	M. pterygoideus dorsalis medialis
ptdmp	M. pterygoideus dorsalis medialis posterior
ptmxp	M. pterygoideus dorsalis, maxillopalatine slip
ptv	M. pterygoideus ventralis
ptvl	M. pterygoideus ventralis lateralis
ptvle	venter externus of M. pterygoideus ventralis lateralis
ptvm	M. pterygoideus ventralis medialis
ptvms	medial slip of M. pterygoideus ventralis medialis
qml	Lig. quadrato-mandibulare
rp	retractor palatini portion of M. pterygoideus dorsalis medialis

Hyoid skeleton figs 25–26

bas	basihyal (N.A.A.: basibranchiale rostrale)
cebr	ceratobranchiale
ent	entoglossum
epbr	epibranchiale
uro	urohyal (N.A.A.: basibranchiale caudale)

Tongue muscles figs 27–30

bmd	M. branchiomandibularis
bmdl	M. branchiomandibularis, lateral origin
bmdm	M. branchiomandibularis, medial origin
cgl	M. ceratoglossus
cglap	aponeurosis of M. ceratoglossus
chy	M. ceratohyoideus (N.A.A.: M. interceratobranchialis)
hyp	M. hypoglossus obliquus
mhy	M. mylohyoideus (N.A.A.: M. intermandibularis)
sehy	M. serpihyoideus
sehya	M. serpihyoideus, anterior slip
sthy	M. stylohyoideus
thy	M. thyrohyoideus (N.A.A.: M. cricohyoideus)
thyd	M. thyrohyoideus, dorsal part
thyv	M. thyrohyoideus, ventral part
trhy	M. tracheohyoideus (N.A.A. nomenclature: see text)

Cervical muscles fig. 31

asc	Mm. ascendentes cervicis (N.A.A.: M. cervicalis ascendens)
co 6–8	M. complexus, slips of origin from vertebrae 6 to 8
itr	M. intertransversarius
rcs	M. rectus capitis superior (N.A.A.: M. rectus capitis dorsalis)
spin	M. spinalis cervicis (N.A.A.: M. longus colli dorsalis)
spla	Mm. splenii accesorii
splc	M. splenius capitis

PART I

Feeding behaviour

This section presents a digest of available information on feeding behaviour in each family, derived largely from a survey of the literature, but also to some extent from personal observations carried out in the course of this study. Some of the latter have already been published at greater length elsewhere (e.g. Burton, 1977, 1979), while others are in preparation. The account given here concentrates mainly on the actions performed by jaws, tongue and neck during feeding. Details of diet and some general ecological background are given, but to pursue these aspects further, it will be necessary to consult the references given.

ALCEDINIDAE

Despite their name, most kingfishers do not fish. Of the three sub-families, only the Cerylinae is exclusively piscivorous. The Alcedininae also hunt mainly by plunge diving, though in several species (e.g. *Alcedo leucogaster*, *A. cristata*, *A. meninting*), it appears that the prey is aquatic insects and other organisms rather than exclusively fish. Some (e.g. *Ceyx* spp.) apparently eat mainly terrestrial or aerial insects. The Daceloninae are predominantly terrestrial feeders, and only a few, notably *Pelargopsis* spp. hunt regularly by plunge diving. Unfortunately, precise information is lacking on the feeding behaviour of most members of this large and diverse subfamily, even such specialized forms as the nocturnal *Melidora*, or *Clytoceyx* which apparently excavates mud for worms with its short but massive bill. Further details on feeding habits throughout the Alcedinidae are provided in the review by Fry (1980).

Whether the prey taken are aquatic or terrestrial, the feeding strategy employed is essentially the same throughout the family; a likely area is scanned from a perch, and periodically a sally is made to capture prey. Searching and sallying are nearly always directed downward to prey on the ground or in the water. A few kingfishers show more versatility; *Halcyon pileata*, for instance, seeks prey with frequent head movements directed to foliage above as well as below (Burton, 1979). Several species capture airborne insects, e.g. *Ceyx* spp., even *H. chloris* (Burton, 1979). Aquatic prey may be sought in hovering flight, particularly among the Cerylinae, notably *C. rudis* (Douthwaite, 1976).

Prey captured are usually large relative to the size of the bird, including reptiles, nestling birds and small rodents in the case of the larger Daceloninae. Capture rates are fairly low, particularly in large species. Prey are commonly beaten against the perch before consumption, with a sharp sideways action. *Dacelo novaeguineae* drops snakes to the ground repeatedly to kill them, and there are records of two individuals cooperating to kill a snake (Keast, 1969). There is some evidence that scorpions may have the sting removed before consumption (Burton 1979, *H. concreta*), but details on the treatment of venomous prey are generally lacking. Fish are swallowed head first, after being oriented along the bill axis. For *A. atthis*, many photographs exist showing fish grasped in the bill (those with the head forward are probably destined for nestlings). In at least some, e.g. Massny (1977), the jaws appear almost parallel, with the lower projecting slightly beyond the upper, evidence of strong retraction of the upper jaw.

Plunge diving, ideally, is accomplished by an almost vertical drop from the perch. However, in species which fish from perches, many dives are strongly oblique. The author has seen *A. atthis* make captures after a slanting flight of nearly 10 metres from a low perch; such instances imply considerable skill in compensating for refraction. There is presumably some relation between the height of dives, and the depth of penetration into the water, though this relationship is unlikely to be a simple one due to habits of prey and availability of perches. However, larger species tend to dive from greater heights than smaller ones, and presumably thus have access to deeper swimming fish. In *A. atthis*, at least, the nictitating

membranes cover the eyes on entry to the water, and if the fish evades capture, inanimate objects may be briefly grasped, suggesting that the prey cannot be seen during the final moments of the attack. The bill is held slightly open as the water is entered (see Junge & Lutken, 1974).

An important use of the bill in all the Alcedinidae is nest excavation. Usually the nest burrow is excavated in a bank of sand or earth. The process has been well described by Eastman (1969). The tunnel is started by flying at the bank and striking it with the bill. Once enough material has been removed to gain a purchase with the feet, excavation continues from a perched position, until the bird is far inside the tunnel, working with the bill, and using the feet to shovel out material. Some kingfishers at least occasionally excavate wood. Excavation of a tree nest site by *H. chloris* has been described in detail by Harrisson (In Smythies, 1960) and England (pers. comm.) kept a pair of captive Kookaburras, *Dacelo gigas*, which cut through an inch thick board of elm wood. The writer has found a nest of *Ceyx pusillus* in the trunk of a rotten tree in lowland rainforest in New Guinea.

TODIDAE

The feeding behaviour and ecology of the todies have been described in great detail by Kepler (1977) from whose paper this account is condensed. Todies forage in a variety of brush or forest habitats, favouring situations with an abundance of twigs, branches and leaves. Insects are captured from all available substrates; in descending order of preference these are leaves, twigs and branches, the air, inflorescences and fruits, and the ground. Perches chosen are those not normally covered by close-touching leaves, and affording a view both above and below. Foraging heights for most species are generally substantially below canopy level; *T. subulatus* forages higher than *T. angustirostris*, and this difference is most marked where both occur together.

Kepler describes two principal feeding methods and three minor ones. Most frequent of all is leaf feeding; the bird perches with bill inclined upwards at angles up to 45° from the horizontal, and scans the undersides of leaves and twigs above it. Seeing an insect, it flies up to the leaf or twig, snaps its bill, and continues in an unbroken arc to another perch. Occasionally insects are taken from the tops of leaves in a downward swoop. Air feeding, second in importance, consists of flycatcher like sallies to capture a passing insect, usually returning to a different perch. Minor feeding methods are hovering in front of feeding substrates, snapping prey from tree trunks, and sliding along perches to glean prey in warbler fashion. After a capture, the insect is usually swallowed in flight, but they kill larger ones either by flicking their heads to and fro or by vigorous beating against twigs for up to a minute.

Feeding rates are greatest in xeric scrub, averaging 1.7 per minute, and slowest in rainforest, averaging 1.0 per minute. Capture rate averages about 41% in dry scrub and 33% in rainforest. Flight distances range from about 1.9 m to 2.6 m., varying somewhat according to species and habitat. Where *T. subulatus* and *T. angustirostris* occur together, the former flies longer distances, illustrating another feature of their behavioural divergence.

Prey recorded for *T. mexicanus* includes 11 insect orders, spiders, and small amounts of miscellaneous items, including plant material. Diptera account for about 31% of the adult diet, and Coleoptera for 23%. Food given to nestlings includes much fewer Diptera, but considerably more Momoptera and Lepidoptera.

The bills are also used for excavating nest tunnels in banks, and occasionally in rotten wood. Sometimes several centimetres of mosses and liverworts have to be torn away to expose the soil. The burrows are usually curved, and Kepler records an average length of 30.5 cm in wet forests, slightly shorter (26.9 cm) in dry scrub. Excavation usually lasts several weeks, the tunnel growing at about 0.5 cm per day. When starting a tunnel, the birds hover in front of the bank, jabbing it with their bills in bouts of 2–5 thrusts. Loose debris is scraped out with the feet, though occasionally large particles may be carried out in the bill.

MOMOTIDAE

Baryphthengus spp. are generally birds of the middle to lower stories of the forest, feeding on large animal prey with some fruits. Johnson (1954) noted *B. martii* in attendance near ant swarms, perching quietly watching for prey animals moving out to escape the ants; these were then taken from tree trunks or palm leaves. One bird which took a large scorpion spent five minutes killing the creature before swallowing it whole; Johnson's account does not mention treatment of the sting. Small lizards, orthoptera, caterpillars, wasps and various fruits are other food items recorded by Wetmore (1968) for *B. martii*.

Closely similar to *Baryphthengus* in diet and habits, *Momotus* spp. range into relatively open areas of second growth or into isolated thickets, as well as forest. Wetmore (1968) and Skutch (1964) record that small birds are exceptionally taken as prey; other items recorded are similar to those listed for *B. martii*. Prey are banded on the perch vigorously and repeatedly, either to quieten them, or to break off wings. Skutch (1964) notes for *M. momota* that seeds of the nutmeg family are swallowed whole, to digest the thin aril surrounding the seed, which is later cast up intact. Though most hunting seems to be done by watching from a perch, *M. momota* may be seen to forage for extended periods on the ground, hopping about with tail cocked up in a manner reminiscent of a thrasher, *Toxostoma*. Skutch (1964) noted an individual of *M. momota* on the ground, apparently searching for a dropped prey item, pushing aside fallen leaves with alternate sweeps of the bill to left and right.

Hylomanes is the least known genus of the family. Wetmore (1968) says it is found alone or in pairs, resting quietly in open undergrowth in humid forest. Prey recorded by him include a spider, a snail, Coleopter, Orthoptera, Homoptera, caterpillars and ants.

Motmots also use their bills to excavate long burrows in earth banks for nesting. An account of excavation in *M. momota* is given by Skutch (1964).

MEROPIDAE

The most thorough survey of Bee-eater feeding behaviour is contained in a comparative study of the various African species by Fry (1972). Except for Asian and Australasian Meropidae, the details which follow are condensed from his account, with extensive verbatim passages.

Small bee-eaters, such as *M. pusillus*, *M. variegatus*, *M. orientalis*, *M. boehmi* and *M. revoli* feed by 'fly-catching'. They keep watch for flying insects from low perches, usually within 2 metres of the ground, and make brief sorties of seldom more than a few metres, returning to the perch with their victim and immobilizing it there. Like all bee-eaters, they are extremely adept at catching the prey, which seldom escapes.

Middle size *Merops*—*M. hirundineus*, *M. oreobates*, *M. bullocki*, *M. bullockoides*, *M. albicollis* and *M. gularis*—also behave like flycatchers, returning to the perch to beat their prey. But they select more elevated vantage points, fly farther after insects, and range more widely, foraging during the course of a day over hundreds of acres or along as much as a mile of wooded watercourses. Upon alighting these species swallow small insects, for example the 5 mm long, stingless 'sweat-bees' (*Trigona* spp.) without treatment, but they immobilize larger insects before eating them. Among *M. bullocki*, the mean of 66 counts of feeding flights, made in and out of the breeding season in all weathers, was 5.2 sorties every 10 minutes. Since these birds average 11 waking hours a day in active feeding and make very few sorties without a capture, an individual *M. bullocki* must eat about 340 insects a day or 124,000 insects a year.

Large birds such as *M. superciliosus*, *M. malimbicus*, *M. apiaster* and *M. nubicus* tend to use tree top perches and to range even more widely, over a few square miles daily. They are also more prone to hunt in continuous flight. *M. apiaster* may be seen twisting and wheeling in flight high over the savannas, catching probably soft-bodied insects such as flying ants and termites. With a large and hard bodied insect, they must return to a perch to immobilize it by beating and if necessary, devenoming it before eating it. (Fry, 1969).

The two species of *Nyctiornis* are less aerial than the smaller bee-eaters. The habits of

N. athertoni are summarized by Smythies (1953); much of its food is obtained while clambering about in trees, taking insects directly from leaves or flowers. Prey include various large insects, such as beetles, in addition to bees. *N. amicta* is more strictly a forest bird, preferring areas where trees are more thinly spaced, especially near the edge of streams or swamps. (Smythies, 1953, 1960; Robinson, 1928). Found in pairs or small groups, it perches at a height of 3 to 6 metres, darting out occasionally to seize prey; it will also clamber about in trees at times like *N. athertoni*. Its flight is noticeably less swift and more laboured than the smaller bee-eaters.

Bee-eaters nest in burrows excavated in cliffs or flat ground. Soil is loosened with the bill and kicked out with the feet; Fry (1972) observes that they will often support the body on a tripod of bill and carpal joints, enabling both feet to be used together. He also notes that a frequent cause of death in all species is getting the head and bill jammed sideways in the tunnel.

LEPTOSOMATIDAE

The little we know of the feeding habits of *Leptosomus* is largely contained in the accounts by Rand (1964), Forbes-Watson (1967) and Appert (1968a). The Cuckoo-roller inhabits forest and brushland, where it stays largely in the tree tops, and is often seen in small parties. According to Rand (1964), the food consists of chameleons, locusts, caterpillars and other large insects. The stomach is often lined with hairs from caterpillars. Large caterpillars, and probably other prey, are held in the bill and beaten against a perch to subdue them before being swallowed.

Forbes-Watson (1967), who watched a nest of *Leptosomus discolor* found that the two young were each being fed six chameleons per day during the period of his observations. He comments that there must either be considerably more chameleons than one would suspect, or the birds must have a large hunting territory and be extremely efficient at finding chameleons. Neither Rand (1964, 1936), Benson (1960) or Forbes-Watson (1967) record other lizards as prey, although Forbes-Watson notes that these were abundant and conspicuous on the ground in the vicinity of the nest he watched. Probably most, if not all, the food, is taken above ground-level. Appert's (1968a) observations give a similar picture except that at a nest he watched, caterpillars seemed to be the main food brought by the male to the incubating female, and by both sexes to the young.

CORACIIDAE

The rollers fall into three distinct groups as regards way of life and feeding behaviour. Typical rollers, *Coracias*, watch for prey on the ground from an elevated perch, fly to seize it, and then consume it there or return with it to the perch; more rarely, they may catch aerial prey, or forage for some time on the ground. Broad-billed rollers, *Eurystomus*, also watch for their prey from a perch, but feed almost entirely on insects captured in flight. When dense swarms pass by, they may stay on the wing for several minutes, making repeated captures while sailing or dashing about with a buoyant and agile flight action. The ground-rollers, confined to Madagascar, are a distinctive group of genera sometimes separated as a family (Brachypteraciidae). They are entirely ground living, and at least some are believed to be partly nocturnal.

Detailed studies of roller feeding behaviour are lacking, though some quantitative information on foraging in *E. orientalis* will be presented in a forthcoming paper on the Artamidae (Wood Swallows) with which it often associates (Burton, in prep.). A good survey of food and ecology in some West African species is given by Thiollay (1971). *Coracias* spp. had taken Coleoptera, Orthoptera, ants and termites in roughly similar quantities; *E. glaucurus* had consumed winged ants and termites in great numbers, but otherwise, prey was predominantly coleopteran. Termites, coleoptera and cicadas are recorded for *E. orientalis*. Other accounts bear out this general picture, though larger prey (scorpions, lizards,

etc.) are often recorded in the case of *Coracias*. Exceptionally, *Eurystomus* has been recorded diving into water to take fish.

Apart from the fact that ground rollers do not normally hunt from perches, prey and feeding methods seem unlikely to differ in essentials from those of *Coracias*. The evidence for their nocturnal habits is partly based on native sources which Rand (1964) considered unreliable, but crepuscular and nocturnal behaviour has been confirmed in *Uratelornis* by Appert (1968b).

Coracias, *Eurystomus* and probably *Brachypteracias* nest in natural cavities, and hence do not use the bill for excavation. However *Uratelornis* certainly excavates a breeding tunnel, and probably also *Atelornis pittoides* (Rand, 1964). The breeding habits of *A. crossleyi* are unknown.

UPUPIDAE

The hoopoe forages principally on the ground, and the following account of its feeding techniques is condensed from the account by Skead (1950). Hoopoes probe assiduously throughout the day, with the bill tip slightly open but not usually penetrating the soil to any great depth in and around grass tussocks. In softer soil the bill may be inserted full length. Prey items are held at the bill tip for a second before being tossed back into the mouth with a short, sharp jerk of the head. Skead once watched a male digging in one spot for five minutes, excavating a hole so deep that his forehead disappeared from view. The prey extracted was pounded heavily on the ground to break it up into pieces small enough to swallow. Hoopoes nearly always probe in short grass rather than long. Probing in wood is rare, but they frequently and successfully probe around the bases of fence posts. Dry cow-pats are flicked over with a deft sideways sweep of the bill, or tipped over backwards. Skead has occasionally seen hoopoes fly up from the ground to hawk flying termites. Prey listed in this and other accounts include a large proportion of insect larvae, especially coleopterous, mole crickets, scorpions and lizards.

PHOENICULIDAE

Unlike the hoopoe, wood-hoopoes virtually never forage on the ground. *Phoeniculus* spp. seek food principally on tree trunks and branches, clambering about over them and probing into crevices and behind loose bark. Prey taken is chiefly insects, including beetles, termites and ants, but small fruits are occasionally eaten. The scimitar bills, *Rhinopomastus* spp., are even more specialized, with a particular fondness for acacias. The behaviour of *R. cyanomelas* is well described by Brown (1969) who writes as follows:

Normally the bird is seen climbing about in the tops of acacia trees, or clinging to the bark as it works up or down, searching minutely for insects. It then behaves more like a creeper or tit than a wood-hoopoe, sometimes hanging upside-down on a branch, or again probing crannies in the bark with head held downwards. When feeding it constantly probes small holes and cracks delicately and gently, or pushes the bill round under stems and the globose flowers of the acacias. Evidently it survives mostly on very small insects.

Brown goes on to describe how the bird works its way along branches of the ant-gall acacia, *A. drepanolobium*, probing with its fine bill into the tiny openings by which ants enter and leave the galls. Presumably small grubs or pupae are obtained in this way.

BUCEROTIDAE

Tockus spp. are generally fairly small and have less enlarged and elaborate bills than most other hornbills. Their diets are wide, and their feeding methods highly versatile. Kemp (1976) has described these in some detail, and distinguishes the following techniques, which are quoted verbatim:

1. PICKING—The food item is picked up where it is found in the vegetation or on the ground, while the bird is standing.

2. DIGGING—Standing on the ground, the bird pushes the closed bill into the substrate and then flicks the dirt to one side, partly opening the bill at the same time. Food items are thus exposed.
3. LEVERING—On the ground, the head is lowered to one side and the closed bill slid under an object. Raising the head causes the bill to work as a lever to turn over the object. This is used when the object is too large to be moved by the digging action, and exposes the food items underneath.
4. CHASING—Pursuing an active food item on the ground.
5. SWOOPING—Flying down from a perch to obtain a food item that has been noticed on the ground below.
6. PLUCKING—Picking up a food item from the ground or vegetation without landing.
7. HAWKING—Catching a flying food item whole on the wing.

Less detail is available for other members of the family, but all authors who have watched large hornbills feeding stress the dexterity and delicacy with which the huge bill can be used. For example, Fogden (1969) writing about *Anthracoceros malayanus* describes a technique used for dealing with potentially dangerous prey such as snakes, centipedes or scorpions. The creature is held by the very tip of the bill and repeatedly squeezed throughout its length, working from end to end several times. The extremities are given a particularly vigorous squeeze, ensuring that the head or tail sting are completely crushed. Objects such as twigs and leaves are often manipulated in 'play' in the same way. Similar dexterity is also shown in dealing with fruits, which the birds are capable of peeling using the bill alone. Objects to be swallowed, whether fruit or animal, are swallowed by tossing them into the air with the bill tip, then shifting the head and open bill to catch them at the rear of the buccal cavity.

This picture generally holds good for most hornbills, whether omnivorous or primarily fruit eaters, but a few show additional specializations. Ground hornbills (*Bucorvus*) are adept at finding and excavating for underground wasps' or bees' nests; honey comb is removed and carried away impaled on the bill tip. *Rhinoplax vigil*, with its relatively short bill and heavy solid casque appears to be adapted for wood excavation, though substantiating field observations are scanty at present.

An activity common to most hornbills though not *Bucorvus* is that of plastering mud or excreta around the entrance of the nest cavity to wall in the incubating female, using the sides of the bill to smear or pat material into place.

GALBULIDAE

Jacamars typically forage in flycatcher style, by making aerial sallies from a perch to catch passing insects. The most detailed published account of feeding behaviour is that for *G. dea* by Burton (1977). This species feeds mainly from relatively high perches at the edges of clearings, rather than from the low perches in scrub or forest favoured by most other jacamars. Feeding flights usually commence with a dive from the perch, followed by a swift pursuit, often involving rapid and agile changes of direction. Occasional flights are made directly upwards. After a capture, the bird returns to a perch with an undulating flight; perches were changed after about 50% of the flights. Flight distances ranged from about 1 to 12 metres, mostly from 4½ to 9 metres, and were of short duration—1.3 to 5.6 seconds, averaging 3.2. Only a single capture occurred in all flights observed. Frequency of flights averaged 21.8 per hour over 5 hours, considerably greater than in *Chelidoptera tenebrosa* (Bucconidae) which feeds by aerial sallies in similar habitat to *G. dea*, and is of similar body size. Prey captured were frequently fairly large, including butterflies, dragonflies and sizable wasps. Large prey were sometimes banged on the perch several times, but back and forth rubbing to devenom Hymenoptera has only been recorded once.

Other species of *Galbula*, and probably also *Brachygalba* and *Jacamaralcyon*, show simbehaviour, though as perches are generally lower, upward flights are more frequent, and perched birds generally sit with the bill inclined upwards at about 45° (about 20° in *G. dea*). Activity rates are probably higher in smaller species; the writer's limited observations on *G. galbula* suggest a flight frequency twice that of *G. dea*, and much more rapid head movements while sitting perched, though the length and duration of flights is generally less. As

in *G. dea*, prey generally seem to average fairly large for the size of the bird, with Hymenoptera predominating. Also, as Wetmore (1968) points out, jacamars are one of the few groups of birds which regularly catch and eat butterflies.

Jacamerops aurea differs from other jacamars in its more sluggish behaviour. Detailed quantitative observations are difficult to compile for this species, which is usually encountered perched moderately high (6 to 10 metres) at the edge of a small clearing in forest. It may sit motionless for several minutes before making a short sally and returning to a new—and frequently invisible—perch. Usually prey taken in these sallies are seized from foliage rather than in flight.

Galbalcyrhynchus, one of the most distinctive genera of jacamars, is also one of the least well known, though it may be surmised that its exceptionally heavy bill denotes a preference for large or hard bodied prey.

Jacamars excavate nest burrows using the bill usually in earth banks. Skutch (1937, 1963), writing about *G. ruficauda*, notes that the bill is used for loosening particles of earth, which are periodically kicked out with the feet, though occasional small lumps are carried out in the bill. Nests are sometimes found in termitaria, though it has not been proved that these were actually excavated by the jacamars themselves in such a hard material.

BUCCONIDAE

A detailed account of feeding in *Chelidoptera* has been given by Burton (1977). This is the most aerial, and one of the most active of puffbirds, resembling more the Wood Swallows (Artamidae) of the Oriental and Australasian regions in its general behaviour and way of life. Most of its prey are small insects, including many Hymenoptera, captured in flight. Though less frequently using agile manoeuvres to catch prey than most jacamars, its sorties are frequently more prolonged, and may sometimes exceed a minute in length, with several captures interspersed by bouts of soaring. Perches commonly used are dead branches near the tops of trees in clearings or at forest edges, on which small groups of the birds often sit close together. Prey are mostly swallowed in flight, and rubbing or beating against the perch was not observed.

Amongst other puffbirds, *Monasa* shows the closest approach to *Chelidoptera* in feeding behaviour (Skutch 1972; Burton, unpubl.), making frequent aerial sallies, which, however, are usually to seize prey from foliage, tree trunks and branches, or sometimes the ground, and less frequently to capture flying insects. They associate in small parties, usually up to a maximum of six and generally return to a new perch after a feeding sortie, with the effect that the whole group gradually moves in straggling fashion through the forest. Sallies usually involve simply a glide on set wings, occasionally with a brief hover as prey is taken, though they are capable of rapid manoeuvring when necessary. Prey include many cicadas, orthoptera, beetles, dragonflies and occasionally butterflies, and also some spiders and millipedes. In contrast to *Chelidoptera*, larger prey are often beaten or rubbed against the perch, for periods of up to a minute. This is by no means confined to venomous species, but if intended to remove wings and legs is not strikingly successful; I have seen even butterflies swallowed whole after a bout of beating. A curious item of behaviour noted by Skutch is the feeding of adult birds by other members of the foraging group.

Nonnula spp. are small members of the family which glean insects off foliage from undergrowth to lower tree crowns, often moving actively through cover as they forage, but sometimes waiting for a time on a perch like other puffbirds. Wetmore (1968) records orthoptera, caterpillars, earwigs, small beetles, membracids and spiders from stomachs. Equally diminutive, *Micromonacha lanceolata* may be similar in habits, though no information is available.

Most other members of the family are larger, more heavily built birds which somewhat resemble forest kingfishers of the genus *Halcyon* in their habits. Normal foraging strategy is to sit on a tree perch at moderate height, motionless but for regular head movements, often waiting for many minutes until prey is seen. After a short flight to seize this, the bird

returns to the same or another perch. Prey taken are usually large insects, obtained mostly from branches or leaves, though *Bucco* spp. perhaps take more from the ground or low herbage.

Puffbirds nest in burrows excavated in earth, or occasionally termitaria. The process of excavation has been observed only in *Notharcus pectoralis* (Skutch, 1948), working on a termitarium. Although this pair were invisible when inside the chamber, Skutch judged from sounds that material was removed by biting or tearing, as well as by hammering. He also notes that in three other species, *Malacoptila panamensis* (Skutch, 1958), *Monasa morphoeus* (Skutch, 1972) and *Chelidoptera tenebrosa* (Skutch, 1948), no excavated earth is found around the burrow entrance, suggesting that this is carried away by the birds. Sticks and dead leaves are placed around the entrance by these three species, a habit especially strongly developed in *Monasa*.

CAPITONIDAE

Barbets occupy a variety of tropical habitats ranging from rainforest to acacia savannahs and dry scrubland. The diet of most species appears to be primarily fruit with some insects, but because of the difficulties of observation in many of their habitats, information on feeding techniques is derived largely from captive birds (See especially England, 1973a & b, 1975, 1976, 1977).

In the wild, the numerous species of figs are probably a major food source for many forest barbets. An interesting photograph in Thomson (1964) shows an individual of *Megalaima zeylanica* carrying four figs simultaneously in its bill. In more open or arid habitats, various berries are recorded, as well as leaves and shoots. Tinker-barbets, *Pogoniulus* spp., often use the berries of mistletoes as a staple item of diet. Insect items recorded include many Orthoptera, as well as beetles, ants, etc. Termites are probably important to *Trachyphonus* spp., at least one species of which nests in termite mounds.

Captive barbets subsist satisfactorily on a variety of prepared fruits, but England notes for several species that the diet switches largely to insects just before and during breeding. It appears that the young are fed mainly on insects at least until the later stages of fledging, as Skutch (1944) observed for *Semnornis frantzii* in the wild. Under aviary conditions, mealworms and locusts are the principal insect food supplied, and their treatment by the barbets is of some interest. Mealworms are often 'mandibulated', that is, crushed and softened by running them from one end to the other several times through the bill tip, which makes many rapid small amplitude bites on the insect. This process is used especially, though not exclusively, when the mealworm is to be fed to fledglings.

Treatment of locusts varies from one species to another. Thus, England (1975) notes that *Eubucco bourcierii* holds the victim on the perch by one foot, or sometimes both, and very occasionally raises a foot to the beak, usually to remove and clasp food which requires more tearing up before swallowing; *Trachyphonus erythrocephalus* holds the locust in its bill by a leg or a wing and shakes it violently until the body comes off, repeating the process until it is devoid of appendages; *Megalaima chrysopogon* seizes and mandibulates the locust, occasionally throwing it up to catch it another way round, then finally swallows it whole. The writer watched *M. zeylanica* and *Psilopogon pyrrholophus* both confronted with a locust for the first time; *M. zeylanica* treated the insect exactly as did England's *M. chrysopogon*, while *P. pyrrholophus* appeared nonplussed, and after a few desultory attacks finally ignored it. More interestingly, a captive specimen of *Semnornis rhamphastinus* treated the locust in a similar way to England's *Eubucco*, using a foot to hold it on the perch. The extraordinary pronged bill tip was then used with great dexterity to systematically pluck all appendages off the locust's body, attacking them near the base, where they were attached to the thorax. The insect was then consumed without further treatment.

Use of the feet has been noted also in *S. frantzii* (Skutch, 1944), which apparently is mainly vegetarian in the wild, consuming fruits, berries and the petals of flowers. Skutch notes that by contrast, *E. bourcierii* in the Costa Rican forests is insectivorous, spending its time well

up among forest trees, where it investigates curled or rolled dead leaves, either probing the interior, or biting them on the outside to drive out prey. The Asian *Calorhamphus fuliginosus* appears to have similar habits, foraging in small parties, and investigating crevices and crannies of all kinds, often behaving in an acrobatic manner more reminiscent of a tit than a barbet (Hume & Davison, 1878). *Megalaima haemacephala* is recorded as making ungainly aerial sallies after insects (Hyatt, in Gooders, 1969–71).

Most barbets use their bills for nest excavation, as well as for feeding. In the great majority, nest holes are bored in rotten timber, even colonially in at least one genus (*Gymnobucco*). *Trachyphonus* spp. excavate in banks, termite mounds, or the ground. The form of the nest chamber and its entrance varies, but it is generally more irregular than those of woodpeckers (Picidae). An account of excavation techniques given for *Tricholaema diadematum* by England (1973a) is probably fairly typical. He writes '... each would attack the wood, hammering away until a piece was loosened at one end; this was then seized and torn off and, when a large beakful was free, it was carried to the far end of the flight and dropped onto an ever-increasing heap. Amazingly, small pieces of wood were swallowed and *regurgitated* on to the heap; practically nothing remained beneath the hole to give the site away to enemies.' Similar techniques have been observed under natural conditions for *Semnornis frantzii* by Skutch (1944). Use of the bill in grasping or consuming wood, and the habit of carrying debris away are important differences from the excavation methods of woodpeckers. Excavation continues during the fledging period as noted by England and by Skutch (1944). The debris thus produced serves the function of soaking up the nestlings' droppings, and soiled wood chips are regularly carried away. In general, the nesting habits of barbets appear more varied and flexible than those of woodpeckers, even if their architecture is less perfect. Fuller details of their interesting breeding biology are given by Skutch, and in the series of papers by England.

INDICATORIDAE

The honeyguides are remarkable for their ability to use wax as a food source (see Friedmann, 1955 for a full account). In the case of the genera *Indicator*, *Melichneutes* and *Melignomon* this is derived from the combs of wild bees; the bees themselves, and their larvae and pupae are also eaten. At least two species of *Indicator*, both African, have evolved a relationship with rats and men in which these predators are guided to the bees' nests by the birds, which can then feed with ease on the remains of the nests after they have been plundered. This is by no means the only food source of honeyguides; a variety of insects are eaten, often captured on the wing.

The smaller sharp-billed Honeyguides (genus *Prodotiscus*) do not attack bees' nests, but nevertheless obtain a considerable amount of wax by eating scale insects (Hemiptera, Homoptera, Coccoidea).

Honeyguides are parasitic in their nesting habits, and the nestlings of at least two species of *Indicator* possess well developed hooks at the tips of both jaws which are used to bite the young of the host, eventually causing death; a detailed account of this behaviour in *I. minor* is given by Friedmann (1955). The hooks are lost early in the fledging period. It is not known whether *Prodotiscus* spp. behave similarly, or possess such hooks, although Maclean (1971) found none in a week old *P. regulus*.

RAMPHASTIDAE

Toucans are primarily fruit eaters, but also take a variety of small animals, including insects, reptiles, and the eggs and nestlings of other birds. Fruits are plucked with the mandible tips, then tossed back with an upward jerk of the head. Despite its size, the bill can be used with some precision, as when birds pass food from one to another. Skutch (1972) suggests for *R. swainsonii* that the size and colours of the bill have an intimidatory value, useful when nest robbing. He also notes that toucans are unable to turn the head back in flight for self defence, a fact which small birds take advantage of when mobbing them. Skutch mentions two

Swainson's Toucans with severely broken bills which nevertheless survived in the wild for at least $2\frac{1}{2}$ years and 7 weeks respectively.

Feeding behaviour is essentially similar in the smaller toucans such as *Aulacorhynchus* spp., and Skutch (1967) has provided a description of nest excavation by *A. caeruleogularis*. Rotten wood was the chosen substrate, and was excavated by pecking and hammering, blows being often (perhaps always) delivered with the jaw tips slightly parted. Only the foreparts were moved when delivering blows, not the whole body. The birds also seemed to bite away pieces of rotten wood. Large billfuls of excavated material were removed at intervals and carried some distance away as in many barbets.

No unusual function in feeding has been ascribed to the exceptionally well developed tongue, although several observers, the writer included, have made a point of looking out for some special form of tongue action.

PICIDAE

The Jynginae (wrynecks) do not excavate, either for food or to make nest holes, but rely entirely on the long protrusible tongue to take food, either from the surface, or from tunnels and crevices. Ants make up a large proportion of the diet of small insects. Though neck movements while feeding appear unremarkable, both threat and courtship displays involve extraordinary contortions of the neck.

Piculets (Picumninae) principally exploit fine twigs, vines, leaf petioles, etc., hammering them in typical woodpecker fashion to gain access to ants and grubs. The tail is not used to prop the body while hammering as in woodpeckers. A good general account of foraging by *Picumnus olivaceus* is given by Skutch (1969). He also quotes Miller (1947) who notes that in Columbia this species shows great versatility, including nuthatch like behaviour in which the bird moves down tree trunks head first. *Sasia* spp. show a fondness for fallen tree trunks and logs, as well as for fine twigs and bamboo. *Verreauxia* evidently forages in a generally similar way to other piculets, but is said to prefer grubs to ants (Bannerman, 1951). All piculets excavate their own nest holes either in trees or bamboo.

Woodpeckers (Picinae) make up the largest of the three subfamilies. They subsist typically on a diet of wood and bark-boring insects, but some, especially *Melanerpes lewis* and *M. formicivorus*, take aerial insects, and other foods include acorns and other nuts, and even cambium and sap, obtained by boring holes through bark (*Sphyrapicus* spp.). The bill is used not only for feeding, but also for nest excavation and to produce 'drumming'—an instrumental sound with territorial significance. An excellent account of both these activities is given by Sielmann (1958). The feeding process also involves sophisticated techniques using the highly modified and protrusible tongue.

A detailed account of woodpecker feeding methods has been given by Spring (1965); an important earlier study was made by Burt (1930). Spring concentrated on three species—*Sphyrapicus varius*, *Dendrocopos villosus* and *Picoides arcticus*. He described the action of hammering carefully, and used ciné photography to assess the contribution of body and neck to the blows. The contribution of the neck was greatest in *Sphyrapicus*, which holds its body closer to the trunk than the other two species; it consequently strikes less powerful blows, but since most of its food is obtained near the surface, deep excavation is not needed. Spring notes that leg and foot adaptations enabling the body to be held well off the trunk impose a penalty of decreased climbing efficiency in the species he studied, but he could not demonstrate any difference in blow delivery between *D. villosus* and *D. pubescens*, or between *P. arcticus* and *P. tridactylus*, despite some anatomical differences. Personal observations of a wide range of woodpeckers seem to indicate that a substantial part of the force of hammering is provided by body movement in a majority of species. An interesting variant of blow delivery is noted for *Campephilus principalis* by Allen & Kellogg (1937) and Tanner (1942). This species forages largely by knocking off flakes of bark with sideways blows to reveal insects underneath.

Several species, notably the Acorn woodpecker *Melanerpes formicivorus* and *Dendrocopos* spp. open nuts, acorns and fir cones by wedging them into cracks or holes in bark, then attacking them with the bill. An interesting account of the development of this behaviour in a captive *D. major* is given by Sielmann (1958). Nuts were carried to the chosen 'anvil' in the bill; if the anvil was inadequate, the nut was held under the breast feathers while the bill was used to chisel out more wood. Pine cones were set upright, and the scales broken off one by one, while seeds were picked out with bill or tongue.

Sielmann (1958) describes the use made of the tongue by several European species as revealed by sophisticated cinematography. A feature of particular interest emerging from these observations is the brief duration of most tongue movements. Although these can be forceful enough to impale beetle larvae, or to create a 'drumming' noise on the side of a box housing a captive *Dryocopus martius*, tongue protrusion is not long sustained, but consists instead of a series of very rapidly repeated darting extensions. Sielmann suggests that this is due not to any inability to maintain the tongue in a state of protrusion, but to the necessity for keeping it adequately coated with the sticky secretion from the highly developed salivary glands.

PART 2

Anatomy

Osteology and arthology of the skull

Literature concerning functional aspects of the skull structure among birds in general is discussed more fully in Part 3 (pp. 399–402), but some important papers may be briefly noted here. Barnikol (1952) dealt with overall form of the skull, Bock (1964) with cranial kinesis and Yudin (1961) with movements of the mandibular rami. Kinetic stops were reviewed by Fisher (1955) and secondary articulation of the mandible by Bock (1960a). The lacrimo-ectethmoid complex was thoroughly surveyed by Cracraft (1968), who should be referred to for details of the complex and its modifications in the various families of Coraciiformes and Piciformes. Studies on probing adaptations in the Charadrii (Burton 1974a) and gaping adaptations in the Icteridae (Beecher 1953a) and Callaeidae (Burton 1974b) are of special relevance to the Upupidae and Phoeniculidae.

Descriptive and comparative cranial osteology of birds belonging to the Coraciiform-Piciform assemblage has been well covered in the literature, although functional studies are mainly confined to the Picidae. A good summary of nineteenth century literature and views is given by Beddard (1898). Many of the papers from this era dwelt largely on palatal structure, pursuing the ideas first introduced by Huxley (1867). Particular attention was given to the woodpecker palate, with discussions by Garrod (1872), Parker (1875) and Shufeldt (1891). Other important studies include those of Murie (1872a & b, 1873) on various Coraciiform families, and of Shufeldt (1884) on *Ceryle alcyon*. Publications on various aspects of osteology in the two orders have continued to appear at intervals in the present century, and most of these are mentioned in the reviews of literature included by Sibley and Ahlquist (1972). Important general studies include those by Lowe (1946, 1948) and Verheyen (1955a & b), while J. Steinbacher (1937) investigated the Galbulidae and Bucconidae, and interest in the Picidae has continued with papers by Burt (1930), Beecher (1953b), Spring (1965) and Zusi & Marshall (1970). The study of rollers, ground-rollers and cuckoo-rollers by Cracraft (1971) included a thorough examination of cranial osteology. A detailed and important work on the skull of a single species of hornbill is that by Manger Cats-Kuenen (1961) dealing with *Rhinoplax vigil*.

Ligaments associated with jaw articulations and other regions of the skull have been surveyed by Lebedinsky (1921) and Bock (1964). Those occurring in the Coraciiformes and Piciformes are listed below; they are present throughout, unless otherwise stated, in which case their distribution is given in the family by family summary of skull morphology which follows.

1. The postorbital ligament runs from the tip of the postorbital process to the external process of the mandible, slightly anterior to its articulation with the quadrate. It is absent or reduced in a number of the families studied here.

2. The occipitomandibular ligament is situated at the dorso-medial edge of M. depressor mandibulae, running from the exoccipital process to the posterior face of the internal process of the mandible.

3. The external jugomandibular ligament is a short band connecting the posterolateral face of the jugal bar with the external process of the mandible. It passes superficial to the postorbital and internal jugomandibular ligaments. It is absent in the Picinae, and very weak in the Jynginae and Picumninae.

4. The internal jugomandibular ligament takes the form of a strong band running around the posterior edge of the interface between quadrate and mandible at their articulation. At its lateral end it is attached to the jugal bar, anterior to the external jugomandibular, and medially to the posterodorsal rim of the mandible. Sesamoid bones are commonly found within the ligament (see e.g. Burton 1973).

5. The quadratomandibular ligament is apparently unique to the Bucerotidae (q.v.). It

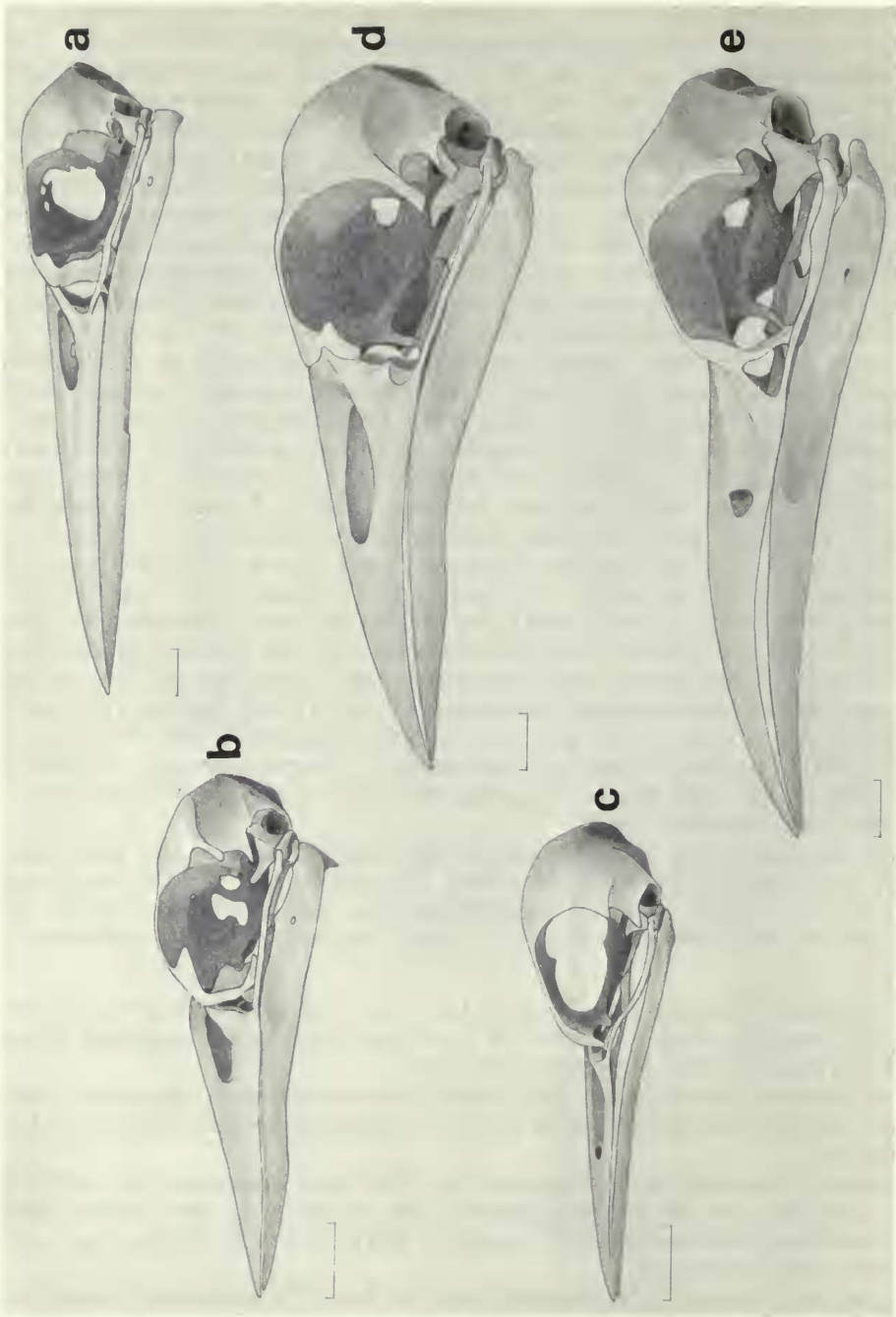


Fig. 1 Skulls in lateral view: a, *Alcedo atthis*; b, *Halcyon concreta*; c, *Todus todus*; d, *Momotus mexicanus*; e, *Nyctornis amicta*. Scale line = 10 mm. in b., 5 mm. in remainder.

runs from the quadrate body to the medial dorsal surface of the mandible, ventral to M. adductor mandibulae externus. (See Starck, 1940: 610).

6. The lacrimojugal ligament, connecting the ventral tip of the lacrimal with the jugal bar, is scarcely defined as such in families surveyed here, although there is normally some connective tissue linkage between the lacrimal-ectethmoid complex and the jugal bar. The lacrimal itself is absent or vestigial in several families of Coraciiformes and Piciformes (Cracraft, 1968).

7. The subocular ligament, running from the lacrimal to the postorbital process is generally represented by a rather diffuse sheet of connective tissue, though in some cases it is strong enough to possess a distinct point of attachment in the form of a small spur on the anterior edge of the postorbital process.

8. The opisthotic ligament, confined to the Picinae, running from the posterior lateral rim of the auditory capsule to the external process of the mandible.

Snap closing jaw ligaments like those described from some Tyrannidae by Bock & Morony (1972) have not been found, though the quadratomandibular ligament of the Bucerotidae occupies a similar situation.

ALCEDINIDAE. Bill generally long and stout (short and deep in *Clytoceyx*), sharply pointed, and with the tomia recurved anteriorly in many Daceloninae. In *Halcyon torotoro* and *H. megarhyncha*, the tomia are irregularly serrated anteriorly. *Melidora* has the upper jaw hooked at the tip, the hook ending bluntly with a U-shaped cross section as in some Buccinidae. Thoroughly desmognathous, the maxillopalatines fused over a considerable distance in the midline. Skull shows some approach to the 'streckschädel' form described by Barnikol (1952) in various fisheaters, with long pterygoids lying in almost the same plane as palatines, sphenoid rostrum and tomia, and the quadrate rotated backwards, its otic articulation lying well posterior to the orbit. This skull form is particularly marked in the Alcedininae and Cerylinae, and the orbital process of the quadrate is narrowed or vestigial in these subfamilies. Medial condyle of the quadrate oval, not remarkably deep. Retroarticular process barely indicated.

Medial brace (see Bock, 1960a) well developed. Postorbital ligament lacking in Alcedininae, feeble or lacking in *Chloroceryle*, fairly stout in Daceloninae.

TODIDAE. Bill long, flattened and rather wide. Not desmognathous, although the maxillopalatines lie close together in the midline. Palatines reduced to frail struts for much of their length. Quadrate with short but broad orbital process, moderately deep, rounded medial condyles. Posterior cranium high, sloping down steeply above the orbits to the fronto-nasal hinge. No retro-articular process.

Medial brace present but feeble. Postorbital ligament narrow but distinct.

MOMOTIDAE. Bill generally robust and somewhat downcurved, with the tomia more or less serrated in their basal two-thirds. The serrations are coarse and tooth like in *Momotus* and *Baryphthengus*, finer (but more numerous) in other genera, especially *Electron*. Unlike many other birds (e.g. toucans) with bill serrations, these projections scarcely slope backwards, but are nearly at right angles to the tomium. In *Electron*, the bill is greatly widened and flattened.

Desmognathous, though midline fusion of the maxillopalatines seems incomplete in some specimens of *Momotus momota*. Quadrate with fairly long but broad orbital process, with an extensive medial edge for attachment of M. pseudotemporalis profundus. Medial condyle oval and deep, extending well ventral to the pterygoid articulation. Postorbital and zygomatic processes strongly developed. Medial brace and postorbital ligament well developed.

MEROPIDAE. The bill is long, moderately decurved and tapering to a sharp point. Fully desmognathous, with a long region of fusion. The posterior cranium extends well posterior to the foramen magnum, and high above the orbit, sloping down very steeply to the fronto-nasal hinge. This profile is less pronounced in *Nyctiornis*, in which the skull is also generally more robustly constructed. Orbital process of the quadrate short and broad, with a long

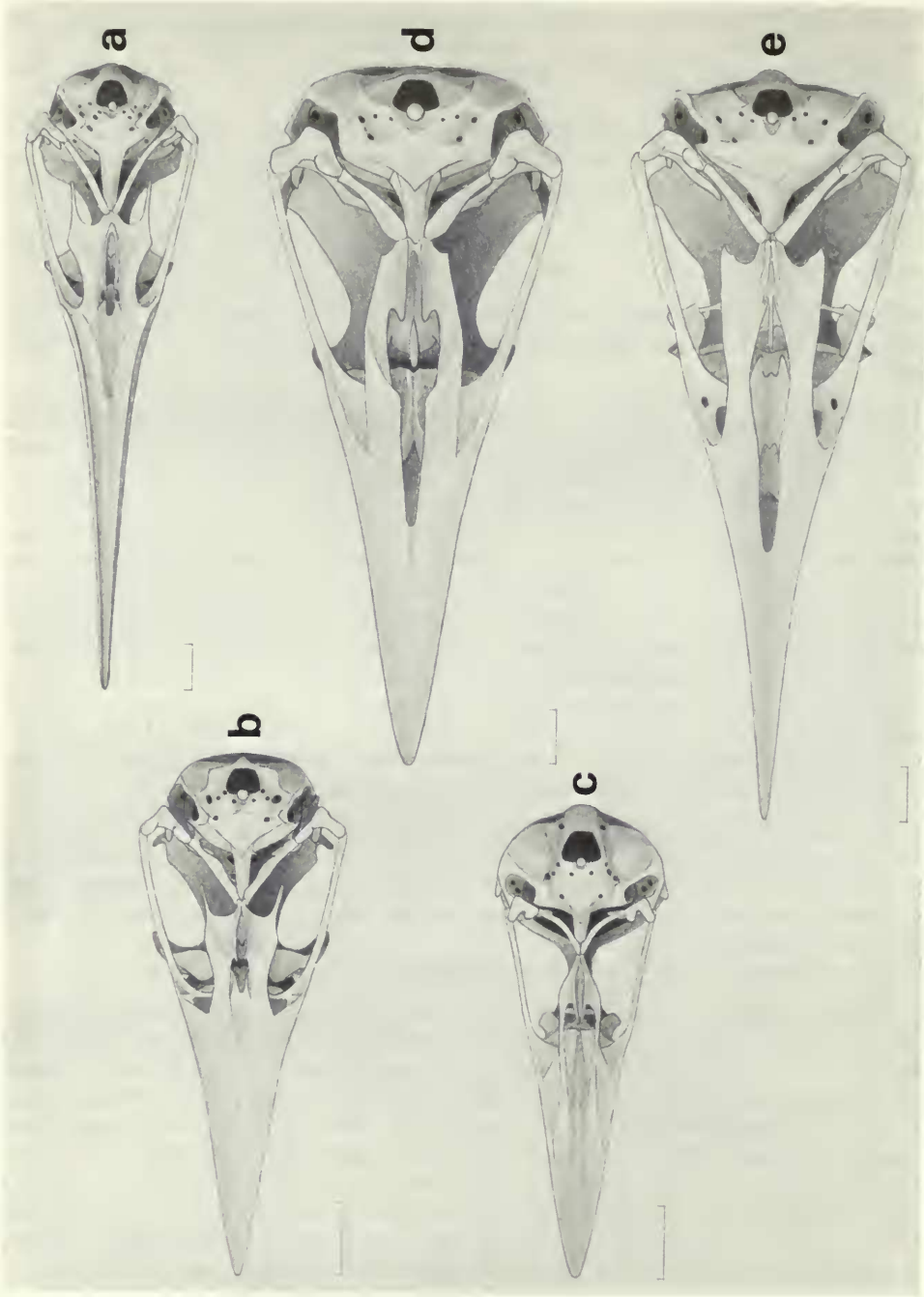


Fig. 2 Skulls in ventral view: a, *Alcedo atthis*; b, *Halcyon concreta*; c, *Momotus mexicanus*; d, *Nyctiorhis amicta*. Scale line = 10 mm. in b., 5 mm. in remainder.

medial edge. Medial condyle a narrow oval in section, and deep, extending well ventral to the pterygoid articulation, and somewhat produced anteriorly to give a hook shaped profile when viewed laterally. No retroarticular process. Medial brace present, postorbital ligament rather weak.

LEPTOSOMATIDAE. The Cuckoo-roller's bill is of medium length and fairly deep, resembling those of typical Coraciidae except in the anterior placement of the nostril. Strongly desmognathous, with wide palatines, and the quadrate with a short, fairly broad postorbital process. Medial condyle oval, rather narrow and deep. Orbits relatively very large. The postorbital process is long, reaching the jugal bar, but without an anterior spur for the suborbital process. No retro-articular process. Postorbital ligament stout; medial brace absent. For a comparison of skull morphology in this and the preceding family see Cracraft (1971).

CORACIIDAE. In *Coracias* and the Brachypteraciinae the bill is typically of moderate length, fairly deep, and with gently decurved tomia. In *Eurystomus* it is shorter, but greatly widened. Completely desmognathous. The quadrate has a short, wide orbital process, and a deep, oval medial condyle. The cranium is generally robust and heavily ossified, with a long, stout post-orbital process, usually reaching the jugal bar, but with a small protuberance anteriorly for attachment of the suborbital ligament. The whole skull is markedly broadened in *Eurystomus*, and its palatines are conspicuously expanded. No retroarticular process. Medial brace well developed, postorbital ligament broad.

UPUPIDAE. Bill long, slender, pointed and decurved, with a heavily developed ramphotheca totally occluding the lumen of the bill for most of its length. Weakly desmognathous, with a narrow zone of maxillopalatine fusion. The quadrate has a short but rather narrow orbital process somewhat expanded at its medial tip, and the thin medial condyle barely projects below the pterygoid articulation. Lateral and posterior condyles are fused into a single crescentic structure. The postorbital process is weak, and lies very close to the zygomatic process. Retroarticular process long, extending well behind the quadrate. Vestigial basipterygoid processes sometimes present.

The postorbital ligament is of moderate breadth and the occipito-mandibular ligament is conspicuously well developed. The medial brace is poorly developed, and oriented more nearly parallel to the long axis of the skull than in other groups.

PHOENICULIDAE. Bill varying from medium length, conical and slightly decurved (*P. aterrimus*) through long and moderately decurved (*P. purpureus*, *P. bollei*) to long, slender and strongly sickle shaped (*Rhinopomastus* spp.); in all cases, the ramphotheca is strongly developed, occluding the lumen as in *Upupa*. Strongly desmognathous in *Phoeniculus*, less so in *Rhinopomastus*. Quadrate orbital process and condyles as in Upupidae, though lateral and posterior condyles are somewhat more distinct. Postorbital and zygomatic processes very close together, the former much reduced. Retroarticular process very long.

Postorbital ligament moderately developed, very strong occipito-mandibular ligament, but medial brace absent.

BUCEROTIDAE. Despite the great variability of the casque in hornbills, the bill itself is rather similar throughout the family moderately long, deep and laterally compressed, with a more or less decurved profile, and tapering to a point. In *Rhinoplax*, the bill is relatively much shorter and more conical than in other hornbills. The skull is robust and heavily ossified, with a doubly desmognathous palate—that is, with maxillopalatines and anterior palatines solidly welded to form a complete bony roof to the proximal part of the upper jaw. The quadrate has a fairly short and rather pointed orbital process. The medial condyle is rounded, but not especially prominent, the lateral crescentic, but clearly distinct from the deeper posterior condyle. Postorbital process well developed. Vestigial basipterygoid processes in some (Starck, 1940). Retroarticular process varying from moderate to barely indicated.

Postorbital ligament extremely broad, occipito-mandibular ligament strongly developed, medial brace absent. In *Bucorvus*, there appears to be some kinetic coupling via the structure

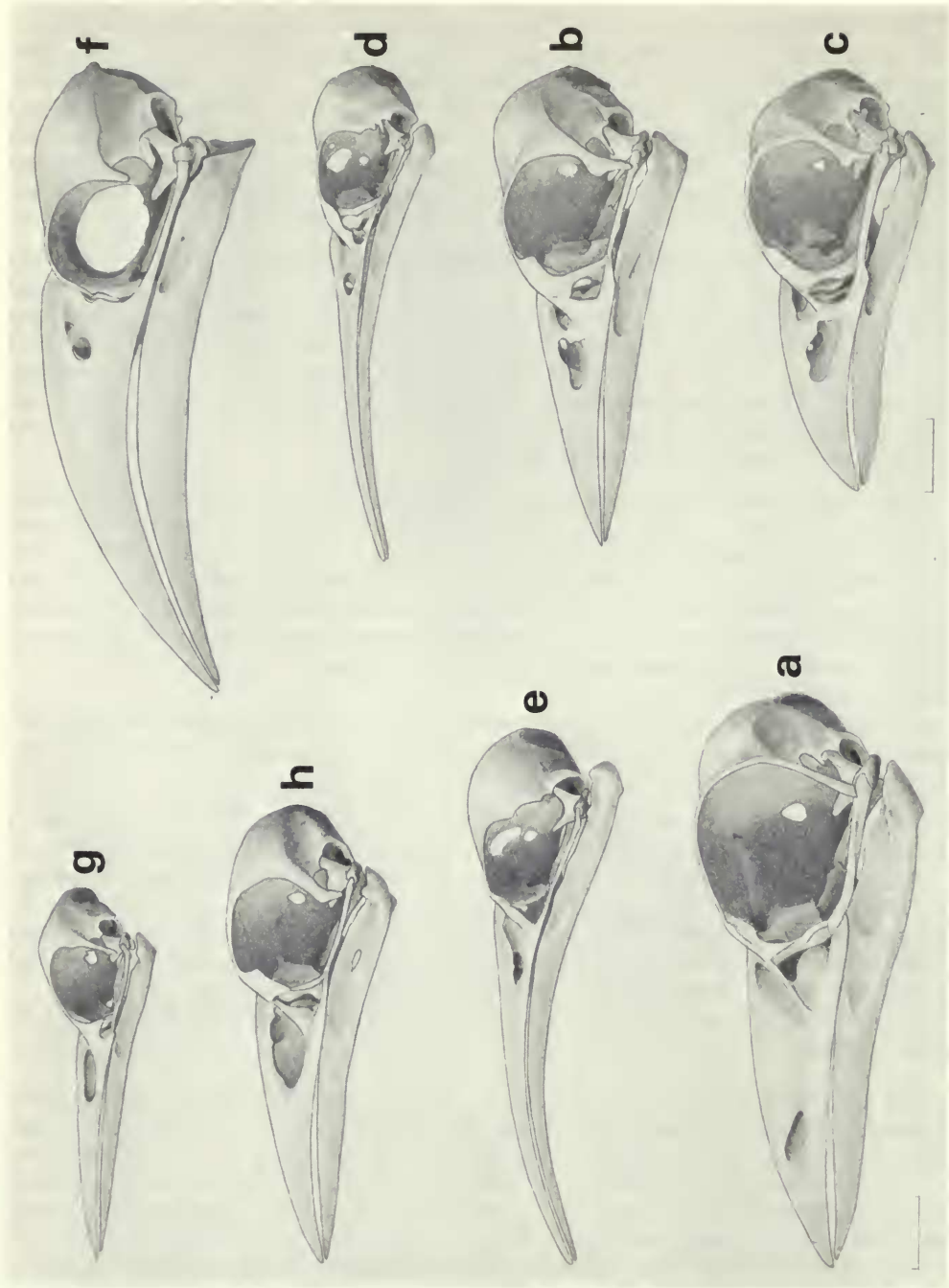


Fig. 3 Skulls in lateral view: a, *Leptosomus discolor*; b, *Coracias benghalensis*; c, *Eurystomus orientalis*; d, *Upupa epops*; e, *Phoeniculus purpureus*; f, *Tockus fasciatus*; g, *Galbula leucogastra*; h, *Monasa atra*. Scale lines = 10 mm: all to same scale.

of the quadrate/mandible articulation; in a dried skull, the lower jaw stays firmly in place once fitted, and in life this would seem to make it impossible for one jaw to move independently of the other. The quadratomandibular ligament appears to be unique to this family, although possibly analogous to one of the snap closing jaw ligaments described by Bock & Morony (1972) in the Tyrannidae.

GALBULIDAE. Bill typically long, slender, sharply pointed and straight. Much deeper and heavier in *Galbalcyrhynchus*, with a strong dorsal ridge; shorter, deep and somewhat decurved in *Jacamerops*. Fully desmognathous, tending to doubly desmognathous in *Galbalcyrhynchus*. Posterior cranium extends well posterior to the foramen magnum, and dorsal to the orbit, producing a sloping profile as in the Meropidae, though less pronounced. This feature is less obvious in the deep billed *Galbalcyrhynchus*, though the rearward projection of the occipital region is still marked. Quadrate with a short and very broad orbital process which has a long medial edge. Medial condyle narrow and deep, extending well ventral to the articulation with the pterygoid. Postorbital process long and stout, nearly reaching the jugal bar. No retroarticular process. Postorbital ligament fairly strong. Medial brace absent.

BUCCONIDAE. Bill very variable in form; heavy, shrike like and slightly hooked (e.g. *Notharcus*); moderately long and slightly decurved (*Monasa*); long and rather flattened (*Nonnula*); short, broad and slightly decurved (*Chelidoptera*). In hook billed types, the hook ends bluntly, with a U-shaped cross section, which may be more or less developed into a notched tip; this is especially well shown in *Notharcus*. The lower jaws of hooked billed puffbirds are often emarginated at the tip.

Strongly desmognathous. Quadrate with a very short but broad orbital process, its wide medial edge nearly in line with the posterior edge, giving a rather pointed appearance. The medial condyle is extremely deep, ending in a rounded tubercle, the lateral and posterior condyles merged. The postorbital process is long, curved and broad, often meeting the jugal bar. No retroarticular process. Postorbital ligament strong. Medial brace absent.

CAPITONIDAE. Bills usually massive, of medium length, but wide and deep, with a strongly curved culmen. *Pogoniulus* spp. have bills of more moderate proportions. Notches or serrations on the tomium of the upper jaw are seen in *Lybius* spp., while in *Semnornis* there is a remarkable arrangement in which the hooked tip of the upper jaw fits into the notched tip of the lower when the bill is closed. *Gymnobucco* and *Stactolaema* spp. have a sharp raised ridge on the base of the culmen in the males.

Most barbets have divided palates, though the maxillopalatines have a narrow region of fusion in some *Pogoniulus* spp., *Capito*, *Eubucco* and *Semnornis*. The vomer has a broad, bifurcated tip resembling that of passerines; hence, the palate may be termed aegithognathous (Beddard, 1898). The quadrate has a long, slender orbital process. The medial condyle does not project far below the pterygoid articulation, but in some species of *Megalaima* it has a sharply defined lateral edge which engages with the lower jaw to give some measure of kinetic coupling. A postorbital ligament is, however, absent in all barbets examined. The postorbital process is long and well defined, and lateral and posterior quadrate condyles are more or less merged into a single S-shaped ridge. The medial brace is absent.

INDICATORIDAE. The bill is of medium length and fairly robust except in *Prodotiscus*, where it is weak and somewhat decurved. The skull is generally similar to that of the Capitonidae, though more lightly constructed and less heavily ossified than in most barbets. The maxillopalatines remain separate; the quadrate has a slender orbital process, a shallow medial condyle, and its lateral and posterior condyles are merged as in barbets. The junction of pterygoid and palatine has a distinctive form (shared with the Picidae), in which the pterygoid foot is elongated, overlapping the posterior end of the palatine dorsally and medially for a considerable distance. The postorbital ligament is weak, but distinct, and the postorbital process well developed. There is no medial brace.

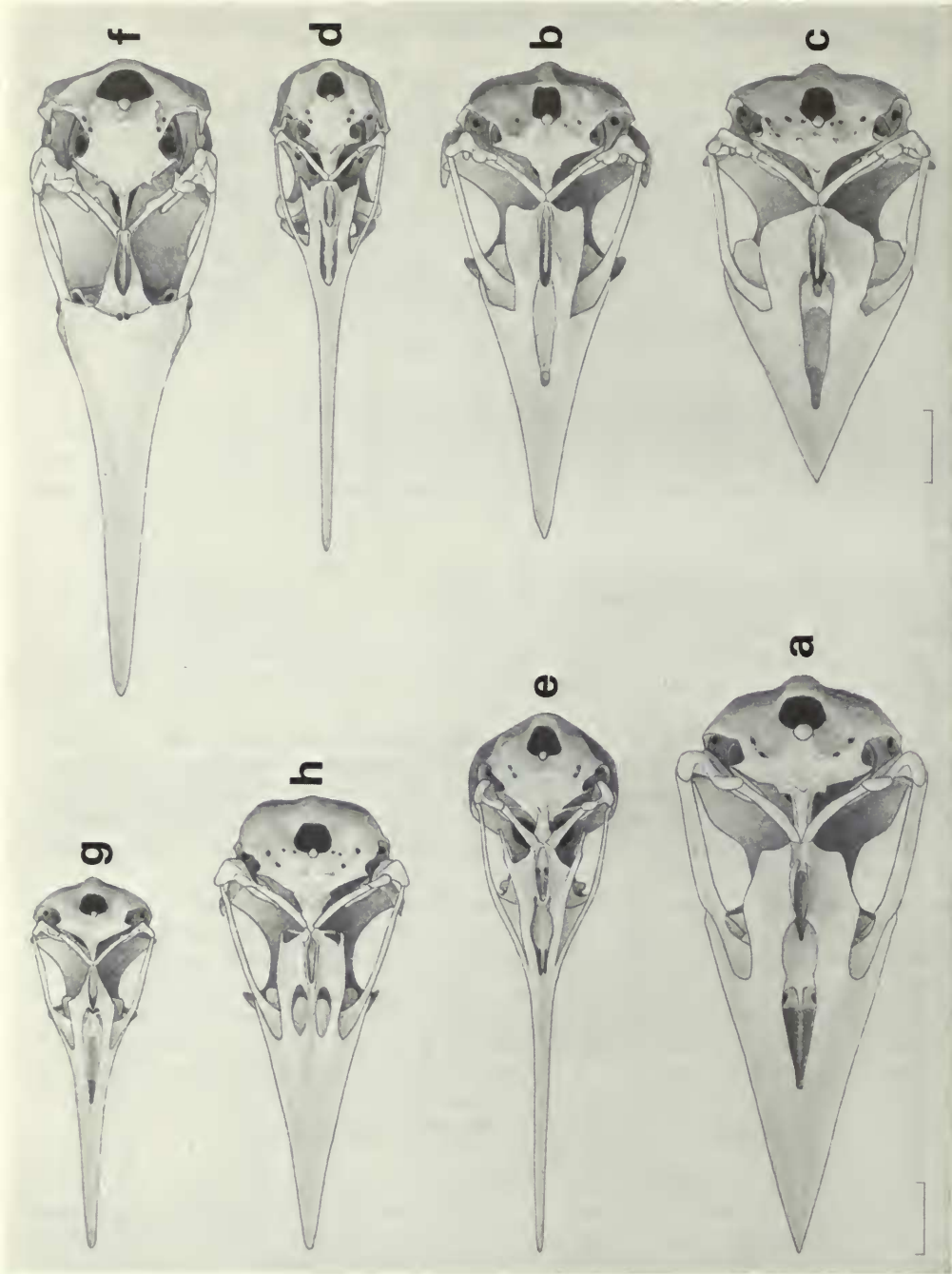


Fig. 4 Skulls in ventral view: a, *Leptosomus discolor*; b, *Coracias benghalensis*; c, *Eurystomus orientalis*; d, *Upupa epops*; e, *Phoeniculus purpureus*; f, *Tockus fasciatus*; g, *Galbula leucogastra*; h, *Monasa atra*. Scale lines = 10 mm: all to same scale.

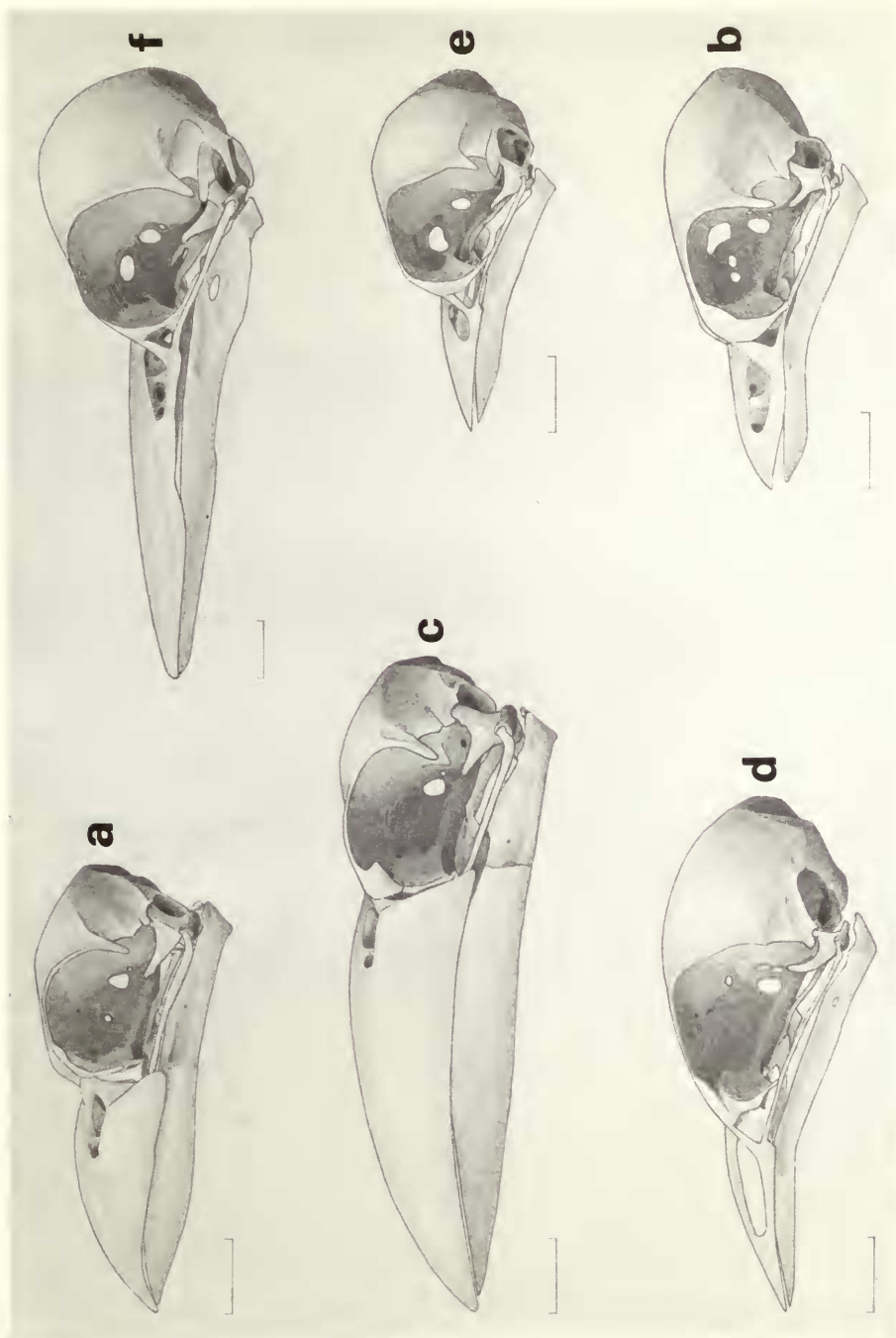


Fig. 5 Skulls in lateral view: a, *Psilopogon pyrolophus*; b, *Indicator minor*; c, *Selenidera langsdorffi*; d, *Jynx torquilla*; e, *Sasia abnormis*; f, *Dendrocopos major*. Scale lines= 10 mm. in a. and c., 5 mm. in remainder.

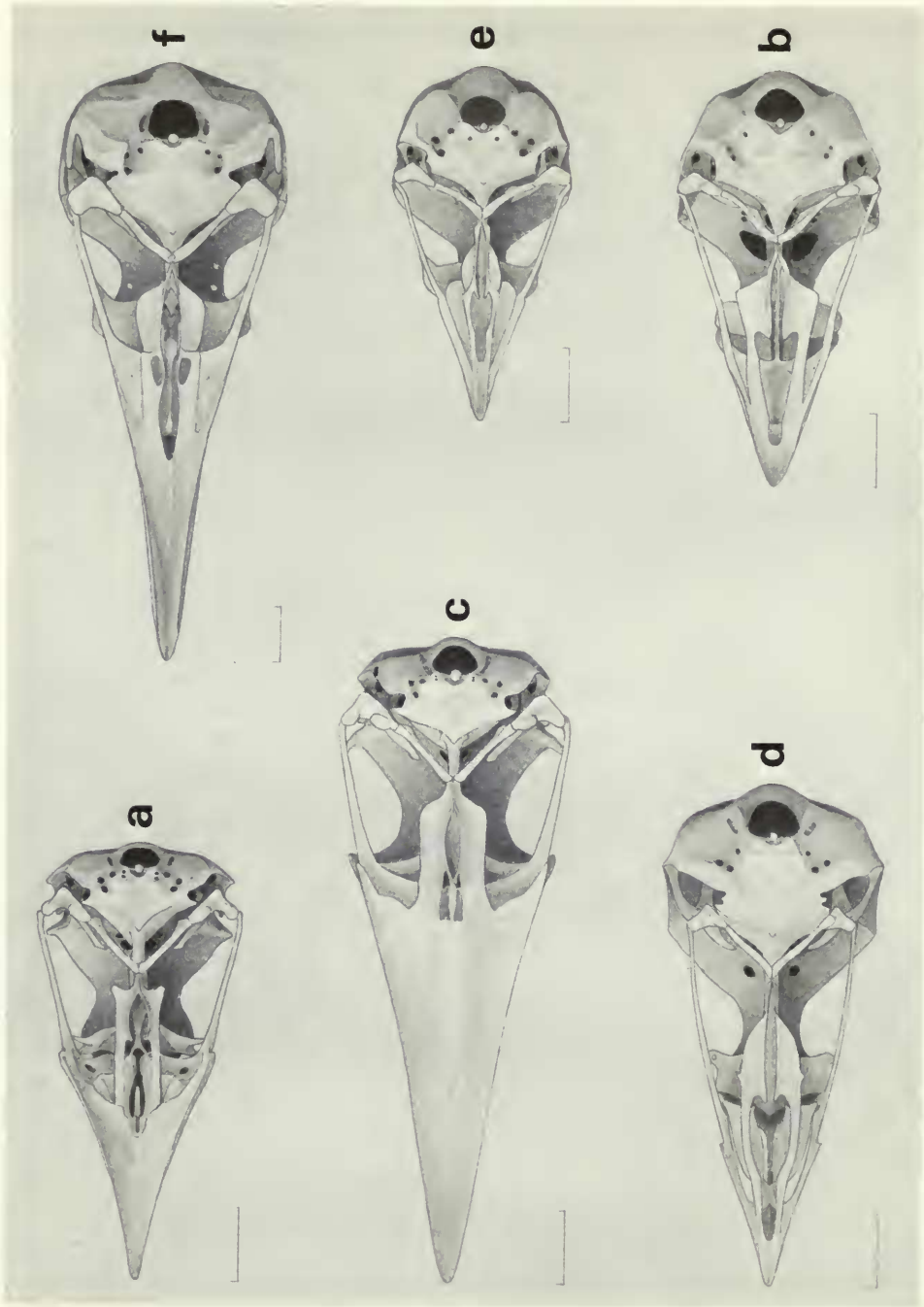


Fig. 6 Skulls in ventral view: a, *Psilopogon pyrolophus*; b, *Indicator minor*; c, *Selenidera langsdorffi*; d, *Jynx torquilla*; e, *Saxis abnormis*; f, *Dendrocopos major*. Scale lines = 10 mm. in a. and c., 5 mm. in remainder.

RAMPHASTIDAE. The use of *R. toco* as an advertising symbol has made the bills of toucans familiar even to non-ornithologists. All are basically similar—long and deep, with a strongly decurved tip. There is less lateral compression than in the superficially somewhat similar bills of the Bucerotidae. The upper tomium is strongly serrated, the lower more weakly; the serrations slope more steeply anteriorly than posteriorly. In *Andigena laminirostris* the tip of the lower mandible ends with a U-shaped cross section which slightly overlaps the curved tip of the upper on each side.

The palate is thoroughly desmognathous, with the maxillopalatines fused along a considerable length of the midline, and the anterior part of the palatines and vomer fused onto the continuous bony sheet lining the upper jaw. As in the Capitonidae the orbital process of the quadrate is long and slender; the medial condyle fairly shallow, and the posterior and lateral condyles merged into a single curved ridge. As in the barbets too, the postorbital ligament is absent, although there is a strong postorbital process. The medial brace is also absent.

PICIDAE. Extensive differences exist between *Jynx* and the remainder of the family. The bills of typical woodpeckers and piculets are short to moderately long, straight, and tapering evenly to a blunt point; the rhamphotheca is hard and well developed. The bills of wrynecks resemble those of woodpeckers in their straight, pointed form, but are proportionately much smaller and more lightly constructed, with large bony nares, and a minimum of rhamphothecal reinforcement.

Other features of skull structure also show considerable disparity between *Jynx* on the one hand and the woodpeckers and piculets on the other. Their principal common features are in palatal structure; all have reduced maxillopalatines and reduced or absent vomer. (For discussion of the latter see Beddard, 1898: 186–187). As in the Indicatoridae the pterygoid foot overlaps the palatine extensively at its posterior end. However, the following specialized features are limited to the Picinae and Picumninae: a pronounced, or even overlapping, forehead at the fronto-nasal hinge; a spur on the pterygoid from which arises part of *M. protractor*; a quadrato-jugal articulation which is extended posteriorly behind the lateral condyle, with consequent enlargement of the quadrate body, especially in the Picinae; and, in the Picinae only, a strong forwardly directed process extending from the posterior lateral rim of the auditory capsule, with ligamentous attachment to the external process of the mandible. In some species this process apparently articulates with the posterior surface of the lateral process of the quadrate, which is markedly broadened in woodpeckers.

The orbital process of the quadrate is long and slender in all three sub-families, but is strongly curved in the Jynginae. The postorbital process and ligament are weak, though distinct, in *Jynx*, but both are quite strongly developed in woodpeckers and piculets. The medial brace is absent in all.

Jaw muscles

The basis for most detailed studies of avian jaw muscles was laid down by Lakjer (1926). His system of nomenclature is adhered to as far as possible, but with modifications stemming from more recent work, notably that of Starck & Barnikol (1954) and Richards & Bock (1973). As noted in the introduction, N.A.A. terms (Baumel *et al.*, 1979) are given in headings where they differ from terms used here. The descriptions given here are effectively the first for most families of Coraciiformes and Piciformes with the exception of those for the Bucerotidae (Starck, 1940) and Picidae (Beecher, 1953*b*).

M. adductor mandibulae externus (abb: M.add.mand.ext.)

This muscle is of complex structure, and several subdivisions can be recognized. Various systems of terminology and criteria have been employed by different authors for naming and distinguishing these subdivisions. The system followed here is that used by Richards & Bock

(1973). Starck & Barnikol (1954) demonstrated the presence of three major aponeuroses in the muscle in birds of several orders. These aponeuroses are recognizable in the families considered here, and the numbering used corresponds to that of Stark & Barnikol. (See also Table 1).

M. adductor mandibulae externus rostralis (M.a.m.e.rost.) is the most dorsal portion of the muscle. It can be further divided into three parts:

(a) *M. adductor mandibulae externus rostralis temporalis* (M.a.m.e.rost.temp.) has a fleshy origin from the temporal fossa, from the base of the postorbital process, and from the dorsal surface of Aponeurosis 2. It inserts on the coronoid process of the mandible via a flattened tendon (Aponeurosis 1) which begins within the temporal region as the raphe of a bipinnate fibre arrangement.

(b) *M. adductor mandibulae externus rostralis lateralis* (M.a.m.e.rost.lat.). Origin is from the lateral edge of the zygomatic process and the dorso-lateral surface of Aponeurosis 2. Insertion is made either through the lateral part of Aponeurosis 1, or through an aponeurosis covering the antero-lateral surface of the muscle, and continuous medially with Aponeurosis 1.

Table 1. Divisions of *M. adductor mandibulae externus* used in the present paper, and their equivalents in some previous studies. Further tables of synonymy are given by Starck and Barnikol (1954). See also Baumel *et al.*, 1979.

	Burton, 1974 (Charadrii)	Starck & Barnikol 1954 (several orders)	Lakjer (1926); Goodman & Fisher, 1962 (Anatidae)
M.a.m.e. rostralis	Part M + Part A dorsal	Aponeurosis 1 portion	Part of superficialis
M.a.m.e. rostralis temporalis	Part M, external temporal	Aponeurosis 1 portion, external temporal	superficialis, 1a portion (Levatoranguli oris).
M.a.m.e. rostralis lateralis	Part A, dorsal	Aponeurosis 1 portion	not present
M.a.m.e. rostralis medialis	Part M, rostral	Aponeurosis 1 portion	medialis
M.a.m.e. postorbital lobe, dorsal part	Not named; absent in most species	Aponeurosis 1 portion	superficialis, 1c portion (retractor anguli oris)
M.a.m.e. postorbital lobe, ventral part.	Not named; absent in most species.	Aponeurosis 1 portion	superficialis, 1b portion
M.a.m.e. ventralis	Part A, ventral	Aponeurosis 2 portion	Included with superficialis 1a portion; rost. temp. + vent. treated as a bipinnate muscle.
M.a.m.e. caudalis	Part B	Aponeurosis 3 portion	<i>M. adductor mandibulae</i> posterior
M.a.m.e. caudilis, lateral expansion	Part B, lateral expansion	Aponeurosis 3 portion	profundus

*In discussions throughout this paper I shall use these terms in their German form, to indicate their origin clearly, to avoid possible ambiguities inherent in their English translations, and because they are less clumsy.

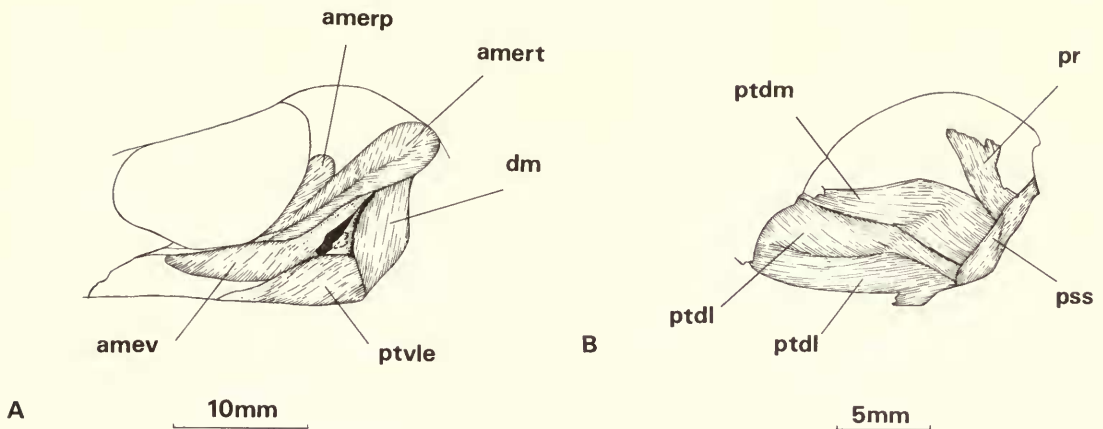


Fig. 7 *Chloroceryle americana*, jaw musculature: A, lateral view; B, dorsal view.

(c) *M. adductor mandibulae externus rostralis medialis* (M.a.m.e.rost.med.) originates from the lateral edge of the posterior wall of the orbit and the medial edge of the temporal fossa. The origin is fleshy, and may also involve an aponeurosis on the medial surface. The insertion is on the anterior coronoid process, posterior and medial to that of *M. adductor mandibulae externus rostralis temporalis*, usually via a lateral aponeurosis which is continuous with Aponeurosis 1.

M. adductor mandibulae externus ventralis. (M.a.m.e.vent.) Origin is from the medial and ventral surfaces of Aponeurosis 2, which begins as a strong flat tendon arising from the zygomatic process, and fans out anteriorly over the lateral surface of the muscle. The main region of insertion is a wide area on the lateral side of the mandible; fibres arising more posteriorly run forwards and downwards to insert on the dorsal surface of Aponeurosis 3 and could equally be considered with M.a.m.e. caudalis.

M. adductor mandibulae externus caudalis. (M.a.m.e.caud.) Origin is fleshy from the otic process of the quadrate, and insertion is usually made principally via Aponeurosis 3 which lies on the dorso-lateral side of the muscle. The insertion is on the dorsal edge of the mandible, behind and below that of Aponeurosis 1. In some species, there is an additional aponeurosis of insertion (Aponeurosis 3a) on the medio-ventral surface of the muscle; it may be separate from Aponeurosis 3 at the insertion, or may fuse with it. There is frequently an additional aponeurosis (Aponeurosis 4) in the muscle, which arises on the otic process, and functions as the raphe of a bipinnate fibre arrangement. In the Picidae, this aponeurosis, and the part of the muscle medial and ventral to it, are expanded anteriorly to insert widely on the lateral surface of the mandible. This will be further explained under the family heading.

CORACIIFORMES

The main general points of difference from the Piciformes concern the lateral region of the muscle. M.a.m.e.rost.lat. is never extensively developed, and in many cases, scarcely to be distinguished. M.a.m.e.vent. fans out further anterior, so that it does not usually conceal M.a.m.e.caud., as in many Piciformes. M.a.m.e.caud. itself is narrow, but usually bipinnate. Aponeurosis 3 may join Aponeurosis 1 medially, and the dorsal edge of Aponeurosis 4 commonly joins Aponeurosis 2 at its medial edge.

ALCEDINIDAE. *Alcedo atthis*. M.a.m.e.rost.temp. is highly developed, the right and left muscles meeting in the midline, at the back of the skull; Aponeurosis 1 extends far back in the temporal region as the raphe of a strongly marked bipinnate system. There is a well developed distinct slip (referred to here as the postorbital lobe) also bipinnate, arising at the

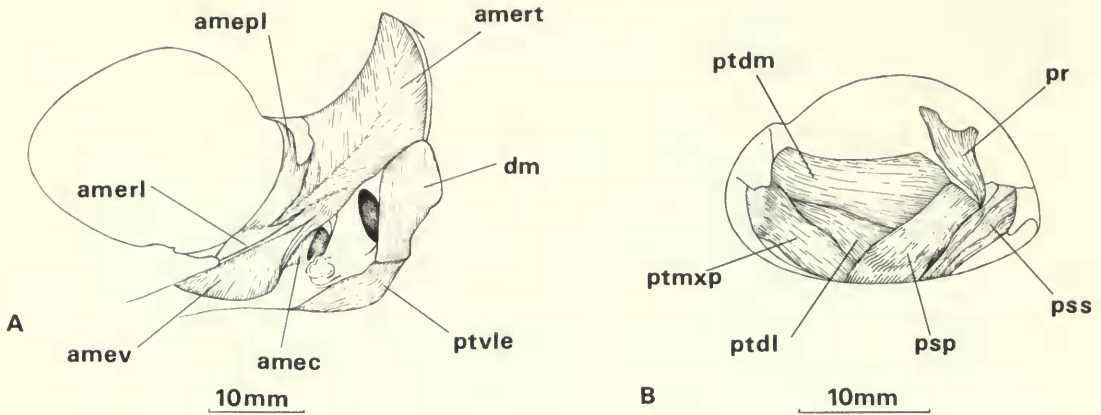


Fig. 8 *Dacelo gaudichaud*, jaw musculature: A, lateral view; B, dorsal view.

lateral edge of the posterior orbital wall, its raphe arising from a blunt process corresponding in position with the postorbital process, the postorbital ligament being absent. The dorso-medial surface of the postorbital lobe is covered by an aponeurosis which joins Aponeurosis 1 anteriorly. M.a.m.e.rost.lat. is absent. M.a.m.e.caud. is small and has only one aponeurosis (Aponeurosis 3), which is vertically oriented. It inserts through this and a small fleshy attachment.

Other members of the family show an essentially similar structure, including a slip arising from the postorbital process, although a postorbital ligament is present in the Cerylinae and Daceloninae. In these families also, a distinct, though small M.a.m.e.rost.lat. can be distinguished, fused posteriorly with M.a.m.e.rost.temp. It is best developed in *Dacelo*, in which it is aponeurotic on its lateral surface, and extends a little way over the dorsal part of M.a.m.e.vent. In the Daceloninae, M.a.m.e.caud. is better developed; Aponeurosis 4 is present and an Aponeurosis 3a was discernible in *Halcyon chloris*.

TODIDAE. *Todus viridis*. The origin of M.a.m.e.rost.temp. is much reduced in extent, but retains clear bipinnate structure. M.a.m.e.rost.lat. is more substantial than in most families of the order, and its aponeurosis of insertion is, in effect, the lateral part of Aponeurosis 1 which has no lateral expansion. Aponeurosis 2 is weakly developed. M.a.m.e.caud. is thin and of simple structure, with only one aponeurosis (Aponeurosis 3). Ventrally and medially there is some fusion with M. adductor posterior.

MOMOTIDAE. *Momotus momota*. M.a.m.e.rost.temp. extends back over about half the cranium posterior to the orbit, but is unusually bulky in the orbital region, bipinnate structure continuing well forward into this area; there is also a small but distinct postorbital lobe. M.a.m.e.rost.lat. is also substantial, and has a strong lateral aponeurosis of insertion. M.a.m.e.caud. is much reduced, and only Aponeurosis 3 can be discerned; this is broad and vertically oriented, its medial edge joining Aponeurosis 1 dorsally. There are no fibres medial to Aponeurosis 3. *Electron platyrhynchum* and *Baryphthengus ruficapillus* are similar, but lack a distinct postorbital lobe.

MEROPIDAE. *Nyctiornis amicta*. M.a.m.e.rost.temp. has a long but narrow area of attachment, extending almost to the midline of the cranium posteriorly. It is strongly bipinnate in structure. Aponeurosis 1 is sharply downturned where it reaches the orbit. M.a.m.e.rost.lat. is vestigial, and M.a.m.e.vent. is thus almost completely exposed laterally. M.a.m.e.caud. is bulky and bipinnate, with three aponeuroses; 3 and 3a which insert separately, though close together, and Aponeurosis 4 arises from the origin, its dorsal edge joining the medial edge of Aponeurosis 2.

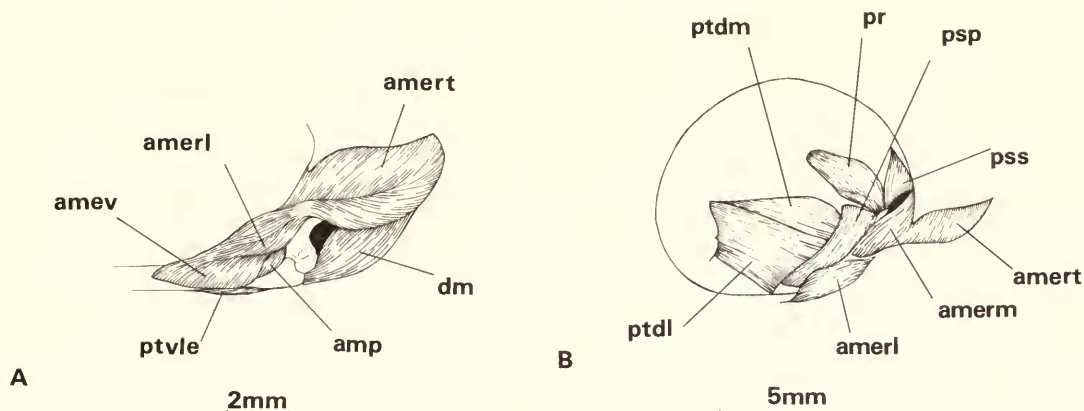


Fig. 9 *Todus todus*, jaw musculature: A, lateral view; B, dorsal view.

Other bee-eaters appear essentially similar. M.a.m.e.rost.temp. is even narrower in other genera, and the downward bend in Aponeurosis 1 at the border of the orbit is absent or unnoticeable. The insertion of M.a.m.e.ext.vent. is generally rather small in extent.

LEPTOSOMATIDAE. M.a.m.e.rost.temp. has a very limited temporal origin, in which no obvious bipinnate structure can be distinguished. Aponeurosis 1 is partially overlapped in the orbit by fibres of M.a.m.e.rost.med. M.a.m.e.rost.lat. is absent. M.a.m.e.vent. possesses the unusual feature of a small aponeurosis on the lateral side arising from the postorbital ligament (which is extremely broad). This joins Aponeurosis 2 anteriorly; it is largely concealed by a lobe overlapping it laterally from below. This lobe consists of fibres inserting on the dorsal surface of Aponeurosis 3, some arising from Aponeurosis 2, and some on the otic process, and hence part of M.a.m.e.caud. The more medial fibres of M.a.m.e.caud. insert along the medial edge of Aponeurosis 3, which is its only aponeurosis in this family.

CORACIIDAE. *Coracias benghalensis*. M.a.m.e.rost.temp. covers about three-fifths of the distance between the orbit and the posterior midline of the skull. Its bipinnate structure is not well marked. M.a.m.e.rost.lat. is absent. M.a.m.e.vent. has a rather small area of insertion, covering only about half the depth of the mandible. M.a.m.e.caud. has a double aponeurosis of insertion (Aponeuroses 3 laterally and 3a medially), the two fusing at the point of attachment. Its fibres are arranged bipinnately about Aponeurosis 4.

In *Eurystomus* M.a.m.e.rost.temp. is more extensive, nearly reaching the skull midline; nevertheless, bipinnate structure is not well marked. The insertion of M.a.m.e.vent. is rather larger, and there is a distinct M.a.m.e.rost.lat.; its fibres are short, arising along the dorsal edge of Aponeurosis 2, and running forwards and up at a steep angle to Aponeurosis 1. *Brachypteracias* is similar to *Coracias*.

UPUPIDAE. *Upupa epops*. M.a.m.e.rost.temp. consists of two portions. The main portion, occupying the temporal fossa, is much reduced by comparison with the majority of families included in this study, the temporal fossa itself being extremely small. An additional portion, corresponding to the postorbital lobe described in the Alcedinidae, arises from the base of the postorbital process, and a concave region on the rim of the orbit just dorsal to this. Both the main portion and the dorsal slip are bipinnate. The strong raphe of the dorsal slip arises from the tip of the postorbital process, anterior to the postorbital ligament, while the raphe of the main portion is, of course, Aponeurosis 1. M.a.m.e.rost.med. is narrow and M.a.m.e.rost.lat. is only moderately developed. M.a.m.e.vent. has the normal wide insertion on the mandible. M.a.m.e.caud. is bipinnate, and has lateral and medial aponeuroses of insertion (Aponeuroses 3 and 3a).

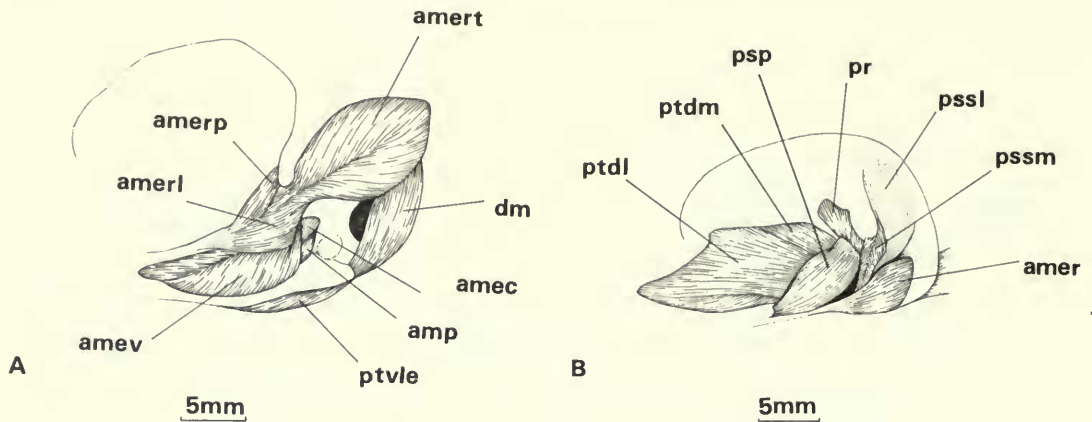


Fig. 10 *Momotus momota*, jaw musculature: A, lateral view; B, dorsal view.

PHOENICULIDAE. *Phoeniculus purpureus*. As in *Upupa*, the postorbital process is relatively close to the zygomatic process, so that the short temporal portion of M.a.m.e.rost.temp. is very narrow. However, the postorbital lobe is bulkier and more complex in structure, consisting of two parts. The more dorsal of these consists of fibres originating dorsal and anterior to the postorbital process, and these insert via an aponeurosis (1a) situated on the dorsal and medial surfaces, on the dorsal edge of the mandible. The more ventral part consists of fibres originating from the ventral surface of an aponeurosis (1b) attached near the base of the postorbital process. This part fans out across the dorsal lateral surface of the mandible, and aponeurosis 1b covers part of this broad fleshy insertion laterally. Aponeurosis 1 itself is broad, and is extended laterally to provide insertion also for the poorly developed M.a.m.e.rost.lat. M.a.m.e.vent. is much reduced by comparison with most birds. Aponeurosis 2 is weak, and the fleshy insertion on the mandible is a narrow one, between the broad fleshy insertion of the postorbital lobe (ventral portion), and the anterior part of M.a.m.e.caud. This latter division of the muscle inserts by two strong aponeuroses (1 and 3a), the dorsal and lateral one (3) attaching just onto the lateral surface of the mandible. Between them lies a raphe (Aponeurosis 4) which spreads out onto the lateral ventral surface of the mandible, the fibres medial to it making a broad fleshy insertion.

P. aterrimus is generally similar to *P. purpureus*, but the following differences may be noted: The dorsal part of the postorbital lobe does not insert only by Aponeurosis 1a, but has in addition a narrow band of fibres extending and inserting along the dorsal lateral edge of the mandible. Aponeuroses 1 and 3 fuse at the insertion; M.a.m.e.vent. is still more reduced. The lateral lobe covered by Aponeurosis 4 is very large, but Aponeurosis 3a is rather weak.

Rhinopomastus resembles *P. purpureus*, but M.a.m.e.vent. is even more reduced, and the temporal origin is almost absent.

BUCEROTIDAE. *Tockus erythrorhynchus*. M.a.m.e.rost.temp. extends back about two thirds of the distance from the orbit to the midline of the cranium. The insertion of M.a.m.ext. on the mandible is narrow, and limited to its dorsal edge. Aponeuroses 1 and 3 are very strong and prominent, and the insertions of both are clearly visible in lateral view. There is no distinct M.a.m.e.rost.lat. A band of fibres arising at the tip of the postorbital process travels a short way to insert at a large angle on the lateral edge of Aponeurosis 1. M.a.m.e.vent. is much reduced, amounting to only a narrow band of fibres inserting between Aponeuroses 1 and 3; Aponeurosis 2 is moderately developed. M.a.m.e.caud. is strongly bipinnate, and the dorsal edge of its raphe (Aponeurosis 4) joins Aponeurosis 2 medially. There is a strong Aponeurosis 3a inserting medial to Aponeurosis 3, and an additional aponeurosis on the medial surface of M.a.m.e.caud.

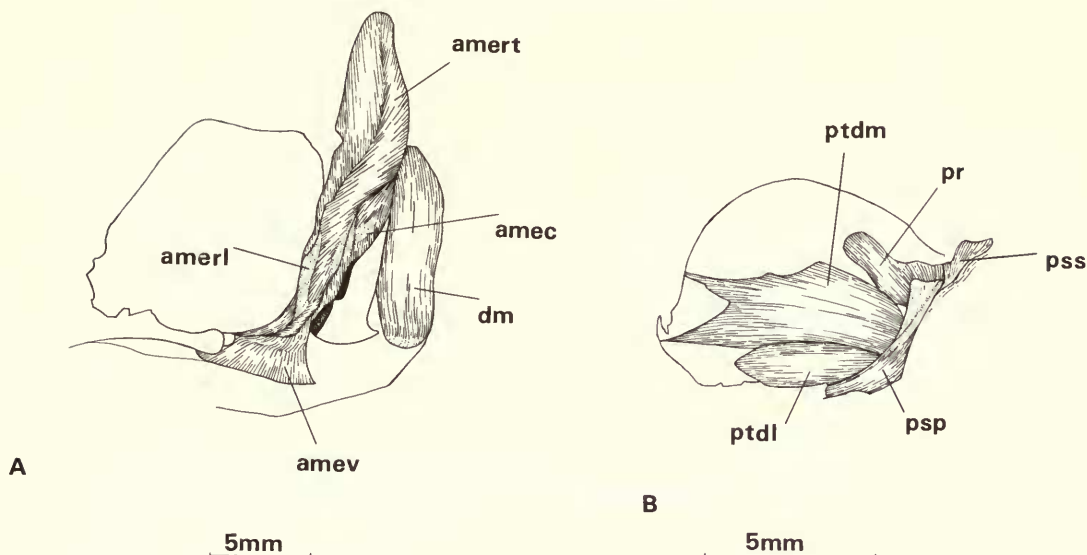


Fig. 11 *Merops superciliosus*, jaw musculature: A, lateral view; B, dorsal view.

PICIFORMES

A feature of the muscle in many Piciformes is the extensive M.a.m.e.lat., which forms a flattened sheet covering much of M.a.m.e.vent., though usually easily separable from it. The anterior part is usually strongly aponeurotic on its lateral surface. M.a.m.e.vent. fans out relatively close to the origin; it frequently conceals the lateral surface of M.a.m.e.caud. Aponeurosis 3 is usually broad, and M.a.m.e.caud. well developed. A raphe (Aponeurosis 4) is often present, but a medial aponeurosis of insertion (Aponeurosis 3a) is lacking in most groups.

GALBULIDAE. *Galbula dea*. M.a.m.e.rost.temp. has a fairly long area of origin covering about three fifths of the space between the orbit and the posterior midline of the skull. Its structure is clearly bipinnate. M.a.m.e.rost.lat. is absent. Aponeurosis 2 is broad, and the fleshy insertion of M.a.m.e.vent. is extensive, but fans out some distance from the origin. M.a.m.e.caud. is bipinnate; its medial fibres insert on a weak Aponeurosis 3a, which dorsally joins the medial edge of Aponeurosis 1 near the insertion. Aponeurosis 3 itself is narrow. Aponeurosis 4 is fairly well developed, joining Aponeurosis 2 dorsally.

These features—which differ in several respects from the general characters of the Piciformes noted above—are shown with little variation by the various other jacamars examined. In *Jacamerops* and *Galbalcyrrhynchus* M.a.m.e.temp. is more extensive, reaching close to the posterior midline of the skull, and Aponeurosis 2 is extensive; In *Brachygalba*, M.a.m.e.temp. is somewhat reduced, covering only about half the posterior cranium.

BUCCONIDAE. *Chelidoptera tenebrosa*. Generally similar to the Galbulidae in most respects. M.a.m.e.rost.temp. extends back about two-thirds of the distance from the orbit to the skull midline. M.a.m.e.vent. is noticeably bulky, but Aponeurosis 2 is not extensive.

Other puffbirds also resemble the Galbulidae (and differ from other Piciformes) in general features. M.a.m.e.rost.temp. reaches the skull midline in *Nystalus* spp. and *Notharcus macrorhynchus*, and nearly as far in *Hypnelos* and *Notharcus tectus*. It is rather short (comparable with *Chelidoptera*) in *Nonnula*. M.a.m.e.vent. is notably bulky also in *Nystalus* and *Notharcus*, and distinctly elongated in *Monasa* spp. M.a.m.e.rost.med. is unusually broad in *Nystalus* spp.

CAPITONIDAE. *Megalaima haemacephala*. M.a.m.e.rost.temp. has an origin extending nearly

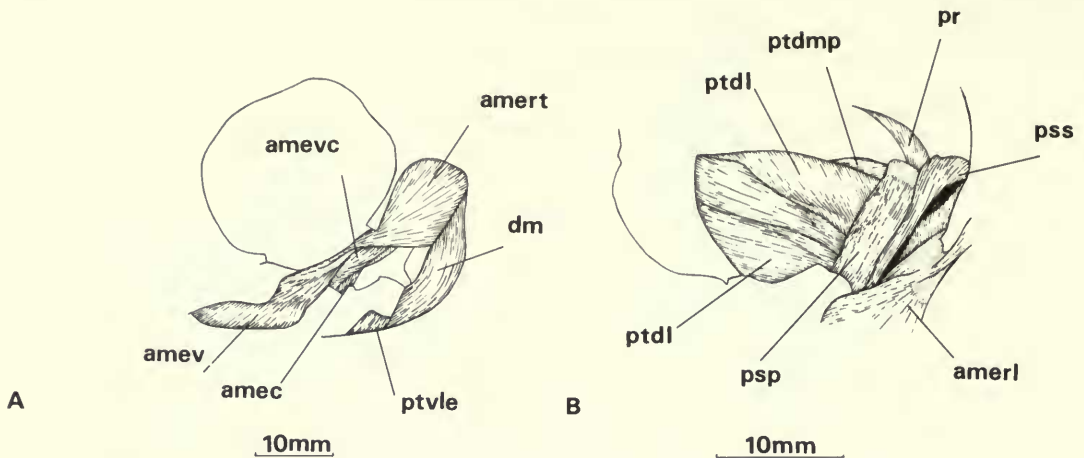


Fig. 12 *Leptosomus discolor*, jaw musculature: A, lateral view; B, dorsal view.

back to the midline, and is clearly bipinnate. M.a.m.e.rost.lat. is wide and flattened, covering more than half the area of M.a.m.e.vent. as seen laterally. Its surface is largely covered anteriorly by a strong aponeurosis continuous dorsally with Aponeurosis 1. M.a.m.e.vent. fans out close to its origin, concealing M.a.m.e.caud. from view laterally. Aponeurosis 3 is broad and vertically oriented, M.a.m.e.caud. forming a rather thin sheet. There is a raphe (Aponeurosis 4), its dorsal edge joining the medial edge of Aponeurosis 2.

The muscle is similar in other barbets examined including *Pogoniulus*. In *Semnornis*, a fleshy slip from M.a.m.e.caud., arising lateral to Aponeurosis 4 extends a short way onto the lateral surface of the mandible.

INDICATORIDAE. *Indicator indicator*. M.a.m.e.rost.temp. extends only about half way to the skull midline. M.a.m.e.rost.med. is bulky, and M.a.m.e.rost.lat. is wide and flattened with an extensive lateral aponeurosis as in barbets. M.a.m.e.vent. has an elongated area of insertion. M.a.m.e.caud. is visible laterally; Aponeurosis 3 is short, and there is a weak bipinnate arrangement, although a clear Aponeurosis 4 cannot be detected. *I. maculatus*, *I. minor* and *Melichneutes* are similar.

RAMPHASTIDAE. *Selenidera maculirostris*. M.a.m.e.rost.temp. spans about three-quarters of the space between the posterior rim of the orbit and the posterior midline of the skull. Aponeurosis 1 is sharply angled down at the edge of the orbit. M.a.m.e.rost.lat. forms a broad flattened sheet as in barbets, but with a more extensive lateral aponeurosis; this covers much of the lateral surface of M.a.m.e.vent. M.a.m.e.caud. is similarly flattened, with a broad, vertically oriented Aponeurosis 3; it is bipinnate, with a distinct Aponeurosis 4, but no Aponeurosis 3a.

Other toucans examined are closely similar.

PICIDAE. *Jynx torquilla*. M.a.m.e.rost.temp. has only a very small area of origin. In the orbital region, Aponeurosis 1 is almost buried by dorsal fibres. M.a.m.e.rost.lat. and M.a.m.e.vent. are similar in their extent and form to those of the Capitonidae and Indicatoridae. M.a.m.e.-caud. is fairly bulky, visible laterally, and weakly bipinnate, though no Aponeurosis 4 can be detected. Aponeurosis 3 is short and superficial, and there is no Aponeurosis 3a.

Dendrocopos major. The origin of M.a.m.e.rost.temp. is small, and there is a vestigial postorbital slip. Aponeurosis 1 is broad dorsally, but partly covered by dorsal fibres; their superficial aponeurosis fuses with Ap.1 anteriorly. M.a.m.e.rost.lat. is fairly narrow. M.a.m.e.vent., also narrow, extends well forward, concealing Aponeurosis 3 which inserts on a prominent ridge on the dorsal lateral surface of the mandible.

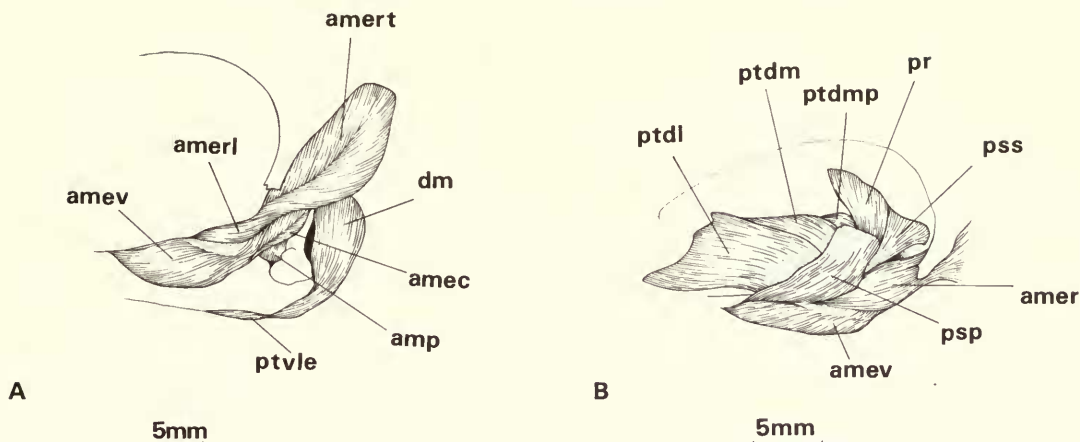


Fig. 13 *Coracias abyssinica*, jaw musculature: A, lateral view; B, dorsal view.

M.a.m.e.caud. is highly developed, and Aponeurosis 4 extends a long way lateral and anterior to the rest of the muscle, with fibres fanning out from its medial surface to insert on the mandible over a wide area ventral and posterior to M.a.m.e.vent. Aponeurosis 3a is broad and strong, inserting posterior and medial to Aponeurosis 3, on the dorsal edge of the mandible.

Other woodpeckers examined—including *Picumnus*—are very similar in all respects. M.a.m.e.caud. is somewhat reduced in *Campephilus malherbi*.

M. pseudotemporalis superficialis

The origin is fleshy, and often also aponeurotic from the posterior wall of the orbit. Insertion is made via a narrow tendon on the dorsal medial surface of the mandible. This typically lies lateral to the bulk of the muscle, whose fibres attach on it in unipinnate fashion. The relationship of the muscle to the course followed by the Vth (trigeminal) cranial nerve is of interest. Typically the nerve lies more or less lateral to the muscle, separating it from *M. adductor mandibulae externus*. In all the families considered here (with a slight modification in some jacamars and puffbirds) the tendon eventually passes medial to the nerve and inserts below it, though this is not so in all bird groups (e.g. some Charadrii; Burton, 1974a).

CORACIIFORMES

In most members of the order, the origin is mainly well to the lateral side of the orbit, and generally rather high. On the medial side there is usually a group of fibres originating considerably lower, but this only constitutes a small proportion of the bulk of the muscle. The Vth cranial nerve usually runs under the muscle towards its *medial* side (not lateral as in most birds), and is unusually near the dorsal surface by comparison with many other groups. The ramus pterygoidei and ramus mandibularis of the nerve typically run close alongside each other for a considerable distance in most members of this order, and the tendon of the muscle in many cases runs between them.

ALCEDINIDAE. The muscle is long and narrow, and its fleshy region extends much further anteriorly than in the other families of the order. In *Alcedo atthis* and *Halcyon chloris* there is a high lateral origin with an aponeurosis along its medial edge from which fibres diverge forwards on each side, those on the medial side coming from a distinct medial lobe with a relatively low origin on the orbit. The Vth cranial nerve runs under this medial lobe. In *Clytoceyx rex* the medial and lateral lobes remain distinct for much of the length of the muscle, and each is bipinnate.

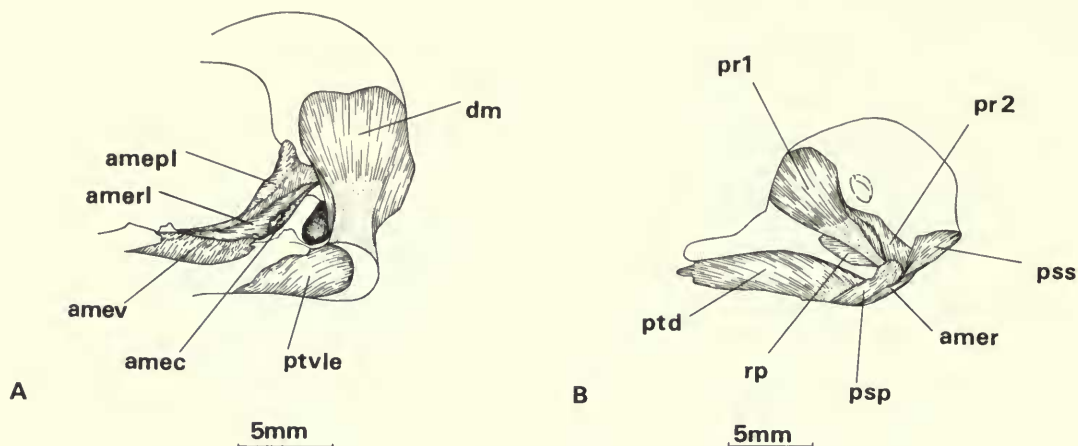


Fig. 14 *Upupa epops*, jaw musculature: A, lateral view; B, dorsal view.

TODIDAE. The muscle is small in size and elongated in shape. Most of its bulk originates fairly high in the orbit; a small region on the medial side originates lower than the rest. The Vth cranial nerve runs along the medial side of the muscle, separating it at the origin from *M. protractor quadrati et pterygoidei*. The muscle is unipinnate in structure, fibres inserting on a lateral aponeurosis. About level with the posterior end of *M. pseudotemporalis profundus* this aponeurosis merges with the long slender tendon of insertion.

MOMOTIDAE. The form of the muscle resembles that of the Todidae, but it is relatively considerably larger, the origin extending high up in the orbit. There is a distinct, though small, medial region with a much lower origin; this is bipinnate in *Momotus* and *Baryphthengus*, but of simple structure in *Electron*. The fibres of the muscle insert on an aponeurosis which cover the whole anterior surface of the muscle, merging into the tendon of insertion about level with the posterior limit of *M. pseudotemporalis profundus*. The Vth cranial nerve runs under the medial edge of the muscle.

MEROPIDAE. Similar to the preceding two families, but ranking between them in the relative size of the muscle and the dorsal extent of its origin. The medial region is very much reduced, and the muscle lies almost entirely lateral to the Vth cranial nerve.

LEPTOSOMATIDAE. The muscle resembles that of the Alcedinidae in form. It is long and narrow, and its fleshy region extends far forward. The lateral origin contributes less to the total bulk of the muscle than in other Coraciiformes. The posterior part of the muscle shows some bipinnate structure about a weak raphe attached to the orbit in the medial third of the muscle. The muscle is joined near its insertion by a slip from the lateral side of *M. pseudotemporalis profundus*. The Vth cranial nerve runs under the muscle towards its medial side.

CORACIIDAE. Similar to the Meropidae in form and situation, but the fleshy region extends further forward—to about the midpoint of *M. pseudotemporalis profundus*—in *Coracias benghalensis* and *Eurystomus glaucurus*. It is smaller, and the fleshy region more limited, in *Brachypteracias squamigera*.

UPUDIDAE. The muscle is bulky and less flattened than in the preceding families, and the Vth cranial nerve consequently lies much deeper. The lateral origin is well developed, and the fibres are attached in unipinnate fashion to a strong lateral aponeurosis which merges into the tendon of insertion about level with the posterior end of the short *M. pseudotemporalis profundus*.

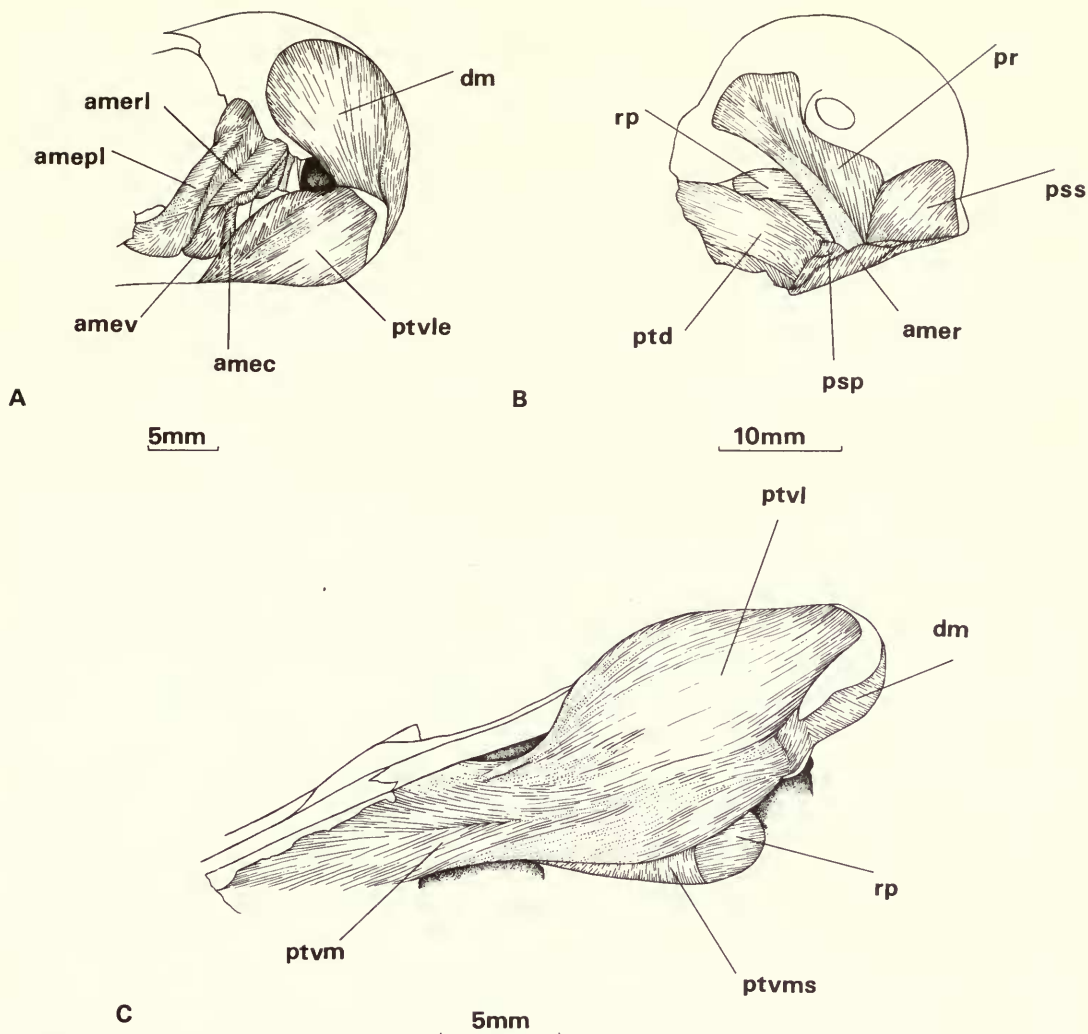


Fig. 15 *Phoeniculus purpureus*, jaw musculature: A, lateral view; B, dorsal view; C, ventral view.

PHOENICULIDAE. Very similar to *Upupa* in both species examined.

BUCEROTIDAE. Similar in form to that of the Upupidae and Phoeniculidae, but the medial edge is strongly emarginated by a crista on the wall of the orbit at about the junction of this muscle and *M. protractor quadrati et pterygoidei*.

PICIFORMES

The origin of *M. pseudotemporalis superficialis* is in general more medially situated than in the Coraciiformes, and never extends very high up the orbit wall. In many species the medial side of the muscle is produced as a narrow extension across part of the origin of *M. protractor quadrati et pterygoidei*. The fifth cranial nerve lies deeper than in most Coraciiformes (except in the Galbulidae and Bucconidae), and generally runs well towards the lateral side of the muscle. The ramus pterygoidei of the nerve usually turns mediad away from the ramus mandibularis after only a short distance, well posterior to the starting point of the muscle's tendon of insertion (except in the Galbulidae, Bucconidae and Picidae).

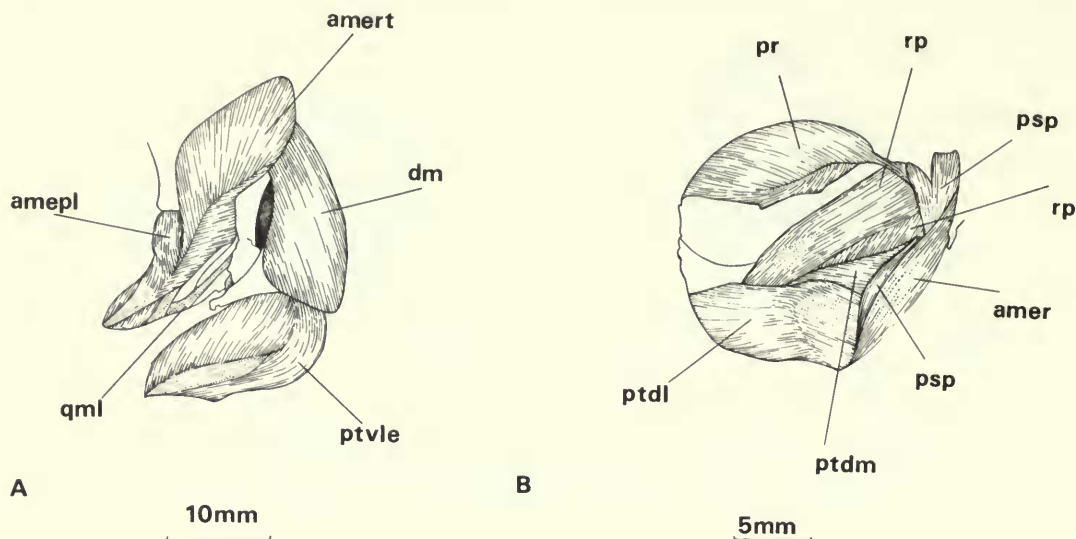


Fig. 16 *Tockus erythrorhynchus*, jaw musculature: A, lateral view; B, dorsal view.

GALBULIDAE. The muscle is vestigial in most jacamars, and entirely absent in one specimen of *Jacamaralcyon*. In this vestigial condition, it consists of a very small and narrow fleshy slip attached low on the orbit wall, immediately lateral to the fifth cranial nerve which, as in the Coraciiformes, lies superficial, with the ramus pterygoidei and ramus mandibularis running close together for some distance. A long and extremely slender tendon beginning level with the posterior end of *M. pseudotemporalis profundus* runs approximately between the ramus pterygoidei and ramus mandibularis of the nerve to insert just below the latter. In *Jacamerops* the tendon is forked at the insertion, one fork passing above the nerve to its attachment. The muscle is best developed—but still very small—in *Galbalcyrrhynchus*.

BUCCONIDAE. The muscle is also vestigial in the puffbirds, and entirely absent in all three specimens of *Nonnula*. In some species (*Notharcus macrorhynchus*, *N. tectus*, *Hypnelus*, *Malacoptila*), it is somewhat better developed, and approximately the shape of an equilateral triangle, though still very small. The form of the fifth cranial nerve, and its topological relations with the muscle are the same as in the Galbulidae. In *Monasa morphoeus* there is a forked insertion like that in *Jacamerops*.

CAPITONIDAE. *M. pseudotemporalis superficialis* is of moderate size, with its origin low on the orbit wall, extending medially to partially cover the origin of *M. protractor quadrati et pterygoidei*. The fifth cranial nerve lies deep on the lateral side of the muscle. The tendon of insertion begins about level with the midpoint of *M. pseudotemporalis profundus*.

The medial extension is particularly marked in *Megalaima haemacephala*. The muscle is bipinnate in *Lybius bidentatus*, the raphe arising from the origin; there is some fleshy insertion as well as tendinous, but all medial and ventral to the ramus mandibularis of the fifth cranial nerve. There is a strong bipinnate medial slip arising from a prominent crista on the orbital wall in *Semnornis*, with a fairly broad fleshy insertion, also medial and ventral to the nerve. A similar condition is seen in *Trachyphonus*, as noted by Starck and Barnikol (1954).

INDICATORIDAE. The muscle is similar in form to that of *Megalaima haemacephala*, with a long medial extension at the origin. It is slightly bipinnate in *I. indicator*, and strongly so in *I. maculatus* and *Melichneutes* in which the raphe arises from a prominent crista on the wall of the orbit. In *I. minor*, however, the muscle is of simple structure, with fibres

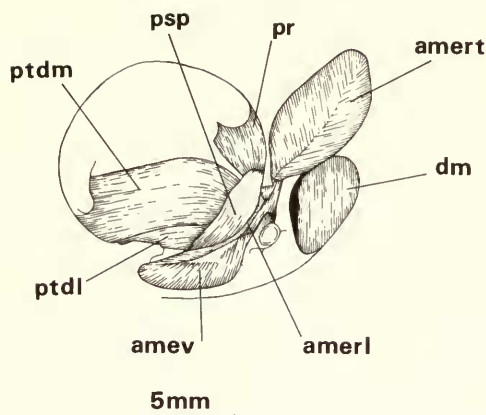


Fig. 17 *Galbula ruficauda*, jaw musculature, dorso-lateral view.

attached in a unipinnate arrangement on the lateral aponeurosis. The fifth cranial nerve, lies lateral to the muscle, and deep. The tendon of insertion begins well forward.

RAMPHASTIDAE. Bulky and bipinnate in the three species examined, but similar in general form to barbets. The raphe is in the medial third of the muscle, arising from a strong crista on the orbit wall. The fleshy part of the muscle extends far forward, and there is a small amount of fleshy insertion additional to the tendon. The fifth cranial nerve runs deep, roughly under the midline of the muscle.

PICIDAE. In *Jynx*, the muscle is of simple structure, with a long medial extension at the origin, much as in *Megalaima haemacephala*. In all Picinae and Picumninae examined, it is triangular in shape, and the origin is more lateral, with no medial extension. It is, however, of simple structure. The fifth cranial nerve runs under its midline.

M. pseudotemporalis profundus and *M. adductor posterior*
(N.A.A.: *M. adductor posterior* = *M. adductor mandibulae caudalis*)

These two muscles are closely associated, both functionally and morphologically, and it is convenient to treat them together. Like *M. pterygoideus*, they both act to lower the upper jaw at the same time that they raise the mandible. Since both attachments of each muscle move, the terms origin and insertion are arbitrary, but following usual practice they are considered as originating on the quadrate and inserting on the mandible. The origin of *M. pseudotemporalis profundus* is a fleshy one from the dorso-lateral surface of the orbital process of the quadrate, and often also from a dorsal aponeurosis attached to the medial edge of the process (generally rather a weak in the birds described here). It is otherwise largely a parallel-fibred muscle although a narrow band of fibres along the lateral or medial edges often shows a unipinnate arrangement.

The insertion is a wide fleshy one on the medial surface of the mandible; the muscle often overlaps the dorsal edge of the mandible to some extent. *M. adductor posterior* takes its origin from the proximal region of the orbital process and from the quadrate body. Lakjer (1926) regarded *N. pterygoideus* as separating this muscle from *M. pseudotemporalis profundus*, and his criterion is followed here, although Stark & Barnikol (1954) have suggested a different basis for discriminating the two. The insertion of *M. adductor posterior* is fleshy, and lies typically on the dorsal surface of the mandible, just posterior to the insertion of *M.a.m.e.-caudalis*, and to the medial surface of the mandible immediately dorsal to that of *M. pterygoideus dorsalis medialis*. However, in many species, there is more or less overlap onto the lateral surface of the mandible, ventral and posterior to the wide insertion of *M.a.m.e.ventralis*.

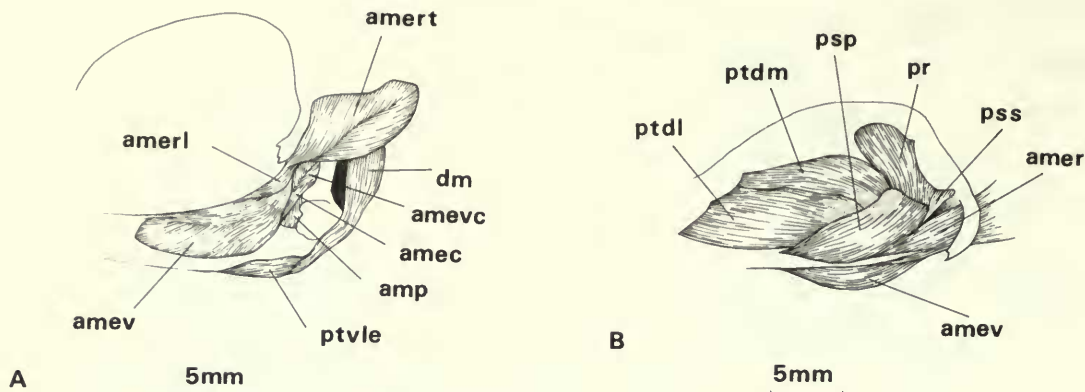


Fig. 18 *Monasa morphoeus*, jaw musculature: A, lateral view; B, dorsal view.

ALCEDINIDAE. *M. pseudotemporalis profundus* is absent in all members of the Alcedininae and several species of Cerylinae. It is, however, present and reasonably well developed in all members of the Daceloninae, and appears particularly broad in *Dacelo gigas*, *D. leachii* and *Clytoceyx rex*. In the Cerylinae, the muscle is absent in all species of *Chloroceryle*, and in *Ceryle rudis*. It is present in *Ceryle torquata*, *C. alcyon* and *C. maxima*; no specimen of *C. lugubris* was available. In these species it is very small, with a narrow and largely aponeurotic attachment to the tip of the orbital process; it is very clearly separated from *M. adductor posterior* by *N. pterygoideus* and loose connective tissue. *M. adductor posterior* is of normal development in all the Alcedinidae, without extensions onto the lateral surface of the mandible. In members of the Cerylinae lacking *M. pseudotemporalis profundus* there is a vestigial, thin orbital process, and the origin of *M. adductor posterior* extends right to its tip; the identity of the more medial fibres is in no doubt, because they are all clearly traversed by *N. pterygoideus*. In the Alcedininae, the orbital process is virtually absent, and the origin of *M. adductor posterior* is consequently limited to the quadrate body.

TODIDAE. *M. pseudotemporalis profundus* appears fairly broad in dorsal view, but there is little indication of a dorsal aponeurosis. *M. adductor posterior* is fairly bulky and just visible laterally under *M. adductor mandibulae externus caudalis*.

MOMOTIDAE. *M. pseudotemporalis profundus* and *M. adductor posterior* are of similar relative development to those of the Todidae in *Momotus* and *Baryphthengus*. In *Electron*, *M. adductor posterior* shows a slight extension onto the lateral surface of the mandible, with a faint aponeurosis at its posterior edge.

MEROPIDAE. *M. pseudotemporalis profundus* is fairly wide, and of even width as seen dorsally. Its dorsal aponeurosis is best developed in *Nyctiornis*, where there is a slight indication of bipinnate fibre arrangement anteriorly. *M. adductor posterior* is invisible in lateral view.

LEPTOSOMATIDAE. *M. pseudotemporalis profundus* is relatively small and narrow. From the lateral edge of the medial tip of the orbital process of the quadrate arises a narrow slip which runs outward to fuse with *M. pseudotemporalis superficialis* near its insertion. *M. adductor posterior* is barely visible in lateral view.

CORACIIDAE. *M. pseudotemporalis profundus* is wide at the origin, tapering anteriorly to a rather narrow insertion. Its dorsal aponeurosis is well developed. *M. adductor posterior* is almost totally concealed in lateral view.

UPUPIDAE. *M. pseudotemporalis* is small and narrow with a weak dorsal aponeurosis, and *M. adductor posterior* invisible laterally.

Phoeniculidae. Similar to Upupa, but *M. pseudotemporalis profundus* rather better developed.

BUCEROTIDAE. *Tockus erythrorhynchus*. *M. pseudotemporalis profundus* is relatively small, and its dorsal aponeurosis is weak. However, it shows a marked bipinnate fibre arrangement about a raphe arising on the orbital process. *M. adductor posterior* is concealed in lateral view.

GALBULIDAE. *M. pseudotemporalis profundus* is fairly small, and *M. adductor posterior* is barely visible laterally.

BUCCONIDAE. In most puffbirds, the medial edge of the post orbital process is long, and *M. pseudotemporalis profundus* is very wide, as viewed dorsally. It is probably best developed in *Nystalus* spp. An exception is *Hypnelus bicinctus*, in which it is relatively much narrower, and the medial edge of the orbital process is shorter than in other members of the family. *M. adductor posterior* is invisible laterally in all species.

CAPITONIDAE. *M. pseudotemporalis profundus* is fairly broad in most species although the dorsal aponeurosis is generally weakly developed, apparently least well developed in *Trachyphonus vaillantii*. *M. adductor posterior* has a small extension onto the lateral surface of the mandible in *Psilopogon pyrrhlophus*, *Semnornis* spp., *Gymnobucco pelli* and *Pogoniulus leucolaimus*; the extension is a moderately large one in *Capito niger*, lying ventral and posterior to *M. adductor mandibulae externus caudalis*.

INDICATORIDAE. *Indicator indicator*. *M. pseudotemporalis profundus* is narrower than in most barbets. *M. adductor posterior* can be seen laterally under *M.a.m.e.caudalis*.

RAMPHASTIDAE. *M. pseudotemporalis profundus* is similar in form and development to most barbets in *Selenidera maculirostris*. In *Ramphastos toco* it appears narrow dorsally, especially at the insertion, but is deep nevertheless. *M. adductor posterior* is just visible laterally in both.

PICIDAE. In all species examined, including *Jynx*, *M. pseudotemporalis profundus* is of moderate size, and *M. adductor posterior* rather small, and invisible laterally.

M. pterygoideus

General structure. Lakjer (1926) recognized four principal divisions of this complex muscle, and his system is followed here. In most of the species examined, the aponeuroses of the muscle correspond closely to those described by Zusi (1962) and Burton (1974) for various Charadriiformes, and these are numbered according to Zusi's system. *M. pterygoideus* normally has its origin on the palatine and pterygoid, and inserts on the posterior part of the mandible. In some birds, a slip from this muscle inserts on the basitemporal plate of the skull. This slip, at one time referred to as '*M. retractor palatini*', is considered under (5) below:

(1) *M. pterygoideus dorsalis lateralis*. (*M. pter. dors. lat.*) This division of the muscle is typically intimately connected with *M. pterygoideus ventralis lateralis*, and the two were thus treated as a single unit by Zusi (1962) and Burton (1974a). Fibres assigned to *M. pter. dors. lat.* are those originating on the dorsal surface of the palatine. They insert on the medial surface of the mandible immediately anterior to those of *M. pterygoideus dorsalis medialis*. The insertion is a broad and fleshy one; an additional surface for insertion is usually provided by a dorsal aponeurosis (*Ap. M*).

(2) *M. pterygoideus ventralis lateralis* (*M. pter. vent. lat.*). Origin is from the lateral edge and caudo-lateral tip of the palatine, usually via a strong aponeurosis (*Ap. A*¹). This aponeurosis generally extends some way across the ventral surface of the muscle, and is often fused with *Ap. A*₂ (see (4)). Its medial edge is commonly infolded, marking the boundary with *M. pterygoideus ventralis medialis*, and acting as a raphe, from which fibres of *M. pterygoideus ventralis* diverge caudad.

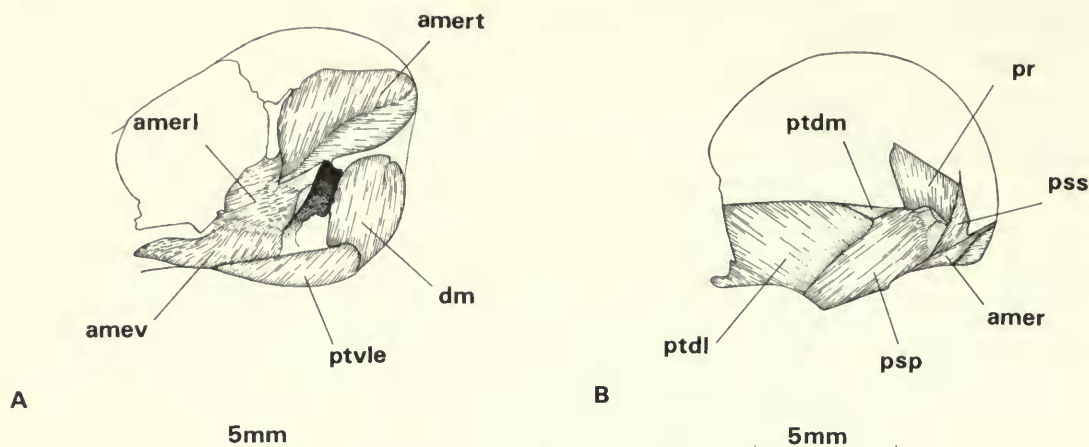


Fig. 19 *Trachyphonus darnaudii*, jaw musculature: A, lateral view; B, dorsal view.

The insertion of *M. pter.vent.lat.* is fleshy, around the ventral edge of the mandible, and commonly on its lateral surface as well. The laterally inserting fibres form a distinct lobe referred to as the 'venter externus' of the muscle (Hofer, 1950).

(3) *M. pterygoideus dorsalis medialis*. (*M. pter. dors. med.*) Origin is principally from the pterygoid, but commonly includes the caudal tip of the palatines. The origin is fleshy, and often aponeurotic as well, and the insertion, at the base of the internal process of the mandible, is fleshy, and also via a dorsal aponeurosis (*Ap. O*). Fibres originating on the antero-lateral face of the pterygoid and on the palatine diverge from those originating on the postero-medial face of the pterygoid. These two areas of the muscle are termed, respectively, *M. pter.dors.med.anterior* and *M. pter.dors.med.posterior* by Richards and Bock (1973). The anterior section is usually much the bulkier of the two. *M. pter.dors.med.* is separated from *M. pter.dors.lat.* by a groove, or sometimes a clear gap, into which, in most birds, the ramus pterygoideus of the Vth cranial nerve passes. In some species, the groove is absent, and the lateral and medial parts of *M. pterygoideus dorsalis* are continuous, as are Aponeuroses *M* and *O*.

(4) *M. pterygoideus ventralis medialis*. (*M. pter. vent. med.*) The ventral surface of the palatine provides the main surface for the origin of this division of the muscle; there is usually also a strong aponeurosis (*Ap. A₂*) attached to the palatine at the anterior boundary of the muscle and continued back some way across its ventral surface. The insertion, on the anterior face of the internal process of the mandible, is partly fleshy, but also includes a strong aponeurosis (*Ap. N*) attached to the medial tip of the process, and running into the muscle as a raphe. The fibres of *M. pter.vent.med.* are oriented more nearly parallel to the long axis of the skull than those of the rest of the muscle.

(5) *Retractor palatini slip*. Attachment of part of *M. pterygoideus* to the basitemporal plate has been reported in the Psittaciformes (Hofer, 1950; Burton, 1974c), Columbiformes (*Didunculus*; Burton, 1974c), Trogoniformes (Burton, 1974c), Bucerotidae (Starck, 1940) and many passerines (Möller, 1930, 1931; Engels, 1940; Fiedler, 1951; Bock, 1960b, etc.). This is clearly a feature which has evolved independently in several lines, and it is therefore not surprising that the structure and origins of the slip vary considerably. It generally derives from part or all of *M. pter.vent.med.*, but may also include fibres of *M. pter.dors.med.* (Bock, 1960b).

CORACIIFORMES

A number of radical modifications in the structure of *M. pterygoideus* occur in this order, of which the most noteworthy are the shift of part of the origin of *M. pterygoideus*

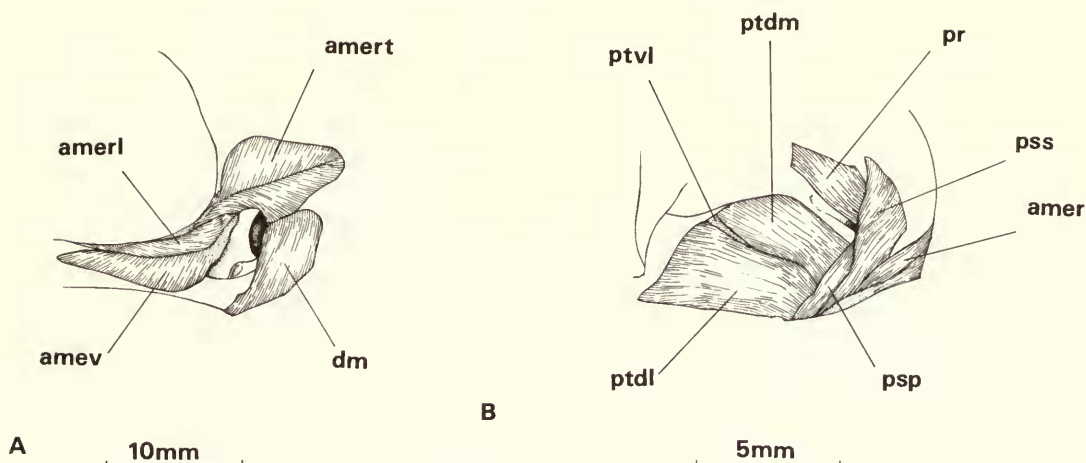


Fig. 20 *Indicator maculatus*, jaw musculature: A, lateral view; B, dorsal view.

lateralis to the maxillopalatine in the Alcedinidae, Phoeniculidae and Bucerotidae; and the development of a large retractor palatini portion in the Upupidae, Phoeniculidae and Bucerotidae.

ALCEDINIDAE. The structure of *M. pterygoideus* in the Kingfishers departs extensively from the general structure given above. In the descriptions which follow, *M. pter.dors.lat* and *M. pter.vent.lat* are considered as a single unit, *M. pterygoideus lateralis* (*M. pter.lat.*) for purposes of clarity.

Alcedo atthis: The groove separating *M. pter.dors.med.* from *M. pter.lat.* is long, and is oriented at only a small angle (approx. 28°) to the midline of the skull. *M. pter.dors.med.* is continued far forward, to the anterior margin of the palatine, which is raised into a prominent crest. *M. pter.lat.* is attached to the palatine fleshily and by a medial aponeurosis to the antero-dorsal crest and the dorsal surface anterior to this. The rest of its attachment is made via a lateral extension of the ventral aponeurosis (ap. A1) to the dorsal surface of the palatal mucosa near the rictus; and to the transverse flange on the ventral surface of the maxilla which marks the posterior limit of the internal ramphotheca of the upper jaw. There is also a small amount of fleshy attachment at the medial tip of the maxillo-palatine. *M. pter.-lat.* is of bipinnate structure. The raphe (which runs approximately along the midline of the muscle) arises from a very strong aponeurosis attached to the lateral surface of the mandible along the dorsal margin of the well developed venter externus; this aponeurosis also gives rise to the dorsal aponeurosis, Ap. M. The raphe is continued, weakening, to the anterior end of the muscle which is forked. The medial fork consists of fibres arising medial to the raphe, and it is this fork which provides the attachments on the palatine and maxillo-palatine. The lateral fork, consisting of fibres arising lateral to the raphe, provides the attachments on the palatal mucosa and maxilla via Ap. I.

The orientation of *M. pter.dor.med.* is nearly the same as that of *M. pter.vent.med.*—a contrast to the majority of birds in which the fibres of the two run at a sharp angle to one another. Consequently the two are largely fused in *Alcedo*. The most distinct part of *M. pter.vent.med.* is the medial region arising on the posterior edge of the pterygoid, and attached on the medial tip of the internal process of the mandible. The rest of the muscle arises by a short aponeurosis from a limited area at the posterior end of the ventral surface of the palatine, and is continuous with *M. pter.dor.med.* above it, its origin being an extensive fleshy one on the dorsal surface of the palatine. The combined *M. pter.med.* is bipinnate about the horizontally oriented raphe Ap. N, fanning out from the medial tip of the internal process of the mandible. Ap. N is situated in the dorsal quarter of the muscle.

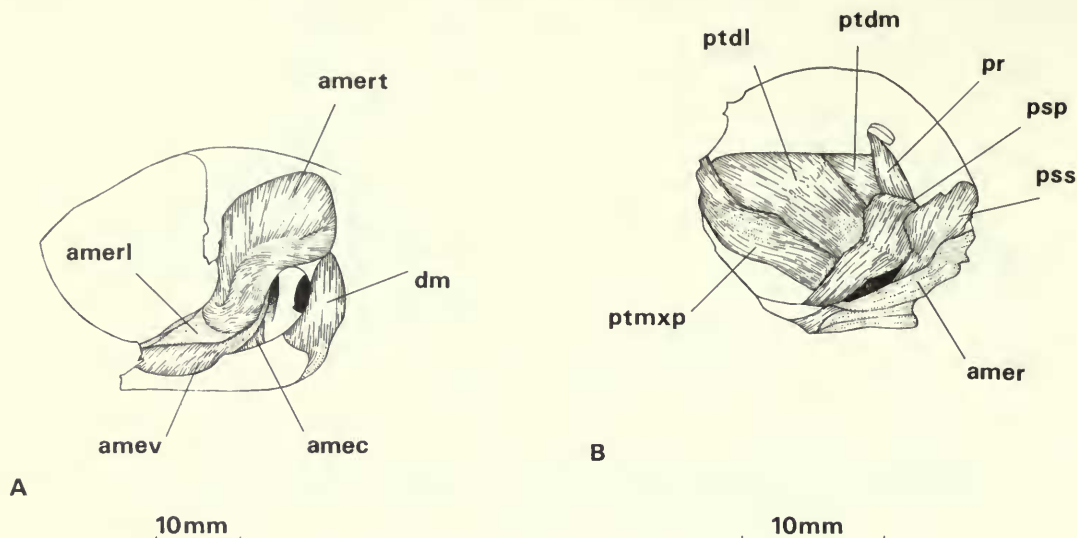


Fig. 21 *Selenidera maculirostris*, jaw musculature: A, lateral view; B, dorsal view.

The structure of *M. pterygoideus* in *Alcedo* may be thus summarized:

M. pterygoideus lateralis: *Origin*: Fleshy and aponeurotic on the antero-dorsal crest of the palatine, the medial tip of the maxillo-palatine, the palatal mucosa and the ventral surface of the base of the maxilla. *Insertion*: fleshy and aponeurotic on the lateral surface of the mandible (venter externus) and a limited region of the ventro-medial surface of the mandible near the base of the internal process. *Structure*: bipinnate about a raphe arising on the lateral surface of the mandible.

M. pterygoideus dorsalis medialis: *Origin*: fleshy on the dorsal surface of the palatine. *Insertion*: on the internal process of the mandible, fleshily and via. Ap. N.

M. pterygoideus ventralis medialis: *Origin*: mainly aponeurotic from the ventral surface of the palatine, and fleshy from the posterior edge of the pterygoid. *Insertion*: fleshy and via Ap. N on the internal process of the mandible. *Structure*: *M. pter. dors. med.* and *M. pter. vent. med.* form a unit which is bipinnate about Ap. N.

Other Alcedinidae: *M. pter. lat.* is of bipinnate structure in all members of the family examined except *Tanysiptera galatea*. The raphe runs roughly along the midline of the muscle in the Cerylinae and Alcedininae, but is shifted more or less to the lateral side in the Daceloninae. The attachment to the maxillo-palatine is small in the Alcedininae, and limited to its medial tip, while in the Cerylinae it is absent altogether. In the Daceloninae, however, this attachment is much more extensive, reaching an extreme in *Dacelo* (especially *D. novaeguinae* and *D. leachii*), *Melidora* and *Clytoceyx rex*. In these species, the attachment is broad, extending over much of the length of the maxillo-palatine, and is made by a dorsal aponeurosis on the posterior edge of the maxillo-palatine, and fleshily on its ventral surface. The attachment to the palatine in these species is extremely limited, and takes the form of a narrow slip, its fibres diverging rostro-medial from those attached to the maxillo-palatine. The main raphe of *M. pter. lat.* in *Dacelo*, *Clytoceyx* and *Melidora* lies lateral and ventral to its position in other kingfishers, so that the remainder of the muscle, attaching on the mucosa and maxilla via Ap. A1 is largely hidden by the more bulky section originating on the maxillo-palatine. In *Tanysiptera galatea* the attachment to the maxillo-palatine is present, and about as well-developed as in most *Halcyon* spp., but the attachment to the mucosa and maxilla is entirely absent.

M. pter. dors. med. extends to the antero-dorsal crest of the palatine in all kingfishers examined. The groove between this muscle and *M. pter. lat.* makes a relatively small angle

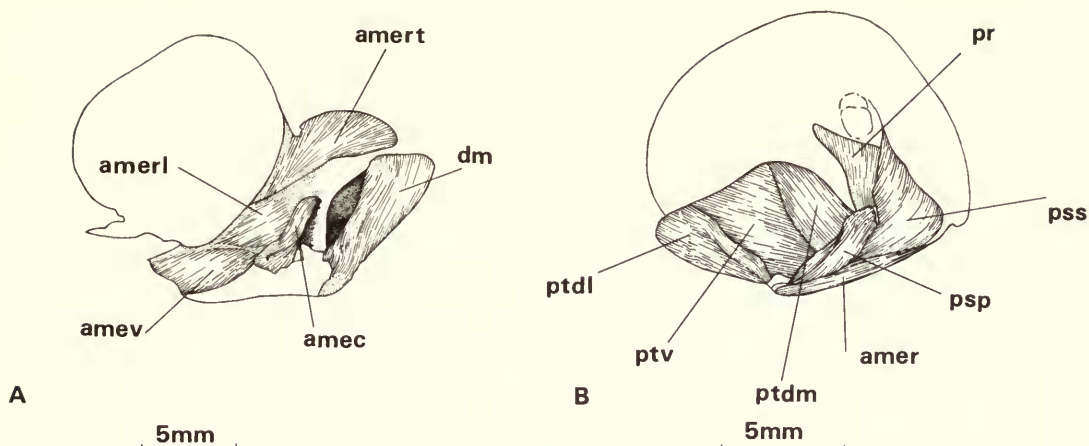


Fig. 22 *Jynx torquilla*, jaw musculature: A, lateral view; B, dorsal view.

to the midline of the skull in all Alcedininae and also Cerylinae (e.g. *Chloroceryle amazona*, 26°). However, among the Daceloninae, the groove is more steeply angled to the midline (i.e. more 'normal') in *Halcyon* and *Tanysiptera* (e.g. 35°, *Halcyon pileata*; 33°, *Tanysiptera galatea*)—in part a consequence of the relatively shorter pterygoids and more posteriorly situated palatines in the Daceloninae. In these genera, the distinction between M.pter.dors.med. and M.pter.vent.med. is clearer, as a result of the different orientation of their fibres. Nevertheless, despite similar skull morphology, *Dacelo* and *Clytoceyx* show the smallest angle of groove to midline of all (approx. 22°–23° in both genera), due to the shift of much of the origin of M.pter.lat. from the palatine to the maxillo-palatine.

In all other features, M. pterygoideus conforms closely to the description for *Alcedo atthis* throughout the Alcedinidae.

TODIDAE. *Todus viridis*. M.pter.dors.lat. is of simple structure, with fibres converging evenly from the origin to the insertion near the base of the internal process of the mandible. M.pter.-dors.med. has origin only from the posterior end of the palatine and the groove separating it from M.pter.dors.lat. is oriented at about 40° to the midline of the skull. The ventral surface of M.pter.vent.med. shows a slight separation of fibres originating on the medial crest of the palatine, and those arising from its ventral surface. There is scarcely any venter externus of M.pter.vent.lat.

MOMOTIDAE. *Momotus momota*. M.pter.dors.lat. is bipinnate, with the raphe well over to the lateral side; part of its origin is on the dorsal surface of the palatal mucosa, lateral to the palatine. M.pter.dors.med. has little attachment on the palatine, and the groove separating it from M.pter.dors.lat. is steeply angled to the midline (approx. 50°). From the ventral aspect. M.pter.vent.med. shows marked separation into a lobe originating on the medial crest of the palatine, and that originating on the rest of the palatine. Most attachment of M.pter.-vent.lat. is at the base of the internal process, including the very strong Ap. M. The venter externus is well developed.

Baryphthengus ruficapillus is very similar. In *Electron platyrhynchum*, however, M.pter.-dors.lat. is of simple structure, and the groove separating it from M.pter.dors.med. runs further anterior, at an angle of about 33° to the midline.

MEROPIDAE. *Nyctiornis amicta*. M.pter.dors.med. extends forward to the antero-dorsal crest of the palatine: the groove separating it from M.pter.dors.lat. is oriented at approx. 30° to the midline. M.pter.dors.lat. itself is of simple structure, and its area of insertion is mainly at the base of the internal process of the mandible. There is hardly any development of the venter externus. Ventrally, M.pter.vent.med. bulges out laterally, ventral to Ap. A1.

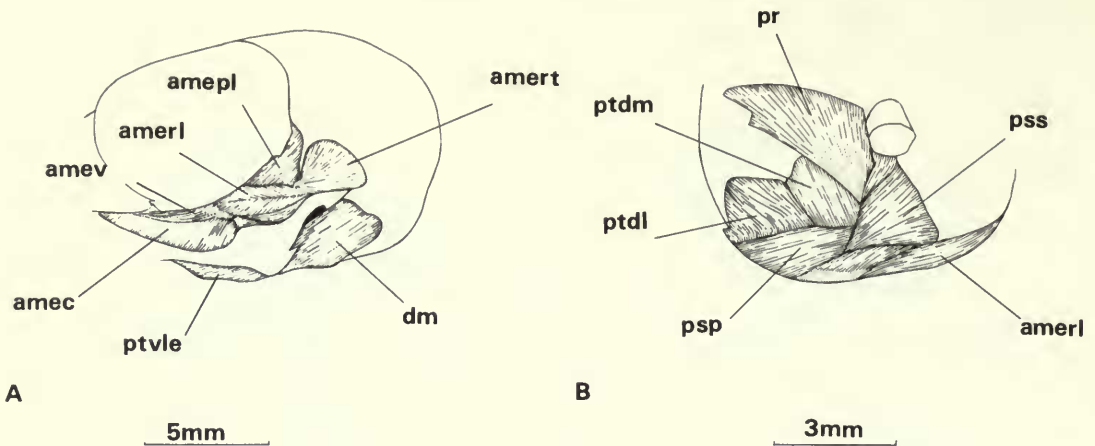


Fig. 23 *Sasia abnormis*, jaw musculature: A, lateral view; B, dorsal view.

Aerops albicollis is similar, but M.pter.dors.med. has even more extensive origin on the palatine, and is clearly broader and more bulky than M.pter.dors.lat. The groove between the two runs at approx. 26° to the midline.

LEPTOSOMATIDAE. Dorsally, no clear groove can be distinguished separating M.pter.dors.lat. and M.pter.dors.med. Both are of simple structure, with fibres converging evenly towards the insertion low on the medial surface of the mandible, and at the base of the internal process. M.pter.vent.lat. has a moderately developed venter externus.

LEPTOSOMATIDAE. M.pter.dors.med. is much reduced. There is a distinct posterior section as in the Coraciidae, and this is the only part of the muscle reaching the basiphenoid rostrum; the anterior section has origin only on the posterior half of the pterygoid, and is concealed by M. pseud.prof. in dorsal view. M.pter.vent.lat. has a small venter externus.

CORACIIDAE. *Coracias benghalensis*. M.pter.dors.med. extends well forward on the palatine, not quite reaching its antero-dorsal crest. The groove separating it from M.pter.dors.lat. is oriented at the relatively shallow angle of 35° to the midline. Fibres of M.pter.dors.med. originating on the postero-medial surface of the pterygoid are angled nearly parallel to the midline, forming a distinct posterior section. There is little development of a venter externus, and the insertion of M.pter.vent.lat. includes the medial surface of the mandible, as well as the base of the internal process. Ap. M. is inserted quite high on the medial surface of the mandible.

In *Eurystomus glaucurus* and *Brachypteracias squamigera*, M.pter.dors.med. also shows a distinct posterior section, but has little attachment on the palatine. The groove between this and M.pter.dors.lat. is steeply angled to the midline (49° in *Eurystomus*, 44° in *Brachypteracias*). There is no venter externus in *Eurystomus*, but a well developed one in *Brachypteracias*.

UPUPIDAE. *Upupa epops*. There is no groove or other indication of demarcation between M.pter.dors.lat. and M.pter.dors.med. The pterygoid ramus of the 5th cranial nerve enters the muscle in a very posterior position immediately level with the anterior edge of the orbital process of the quadrate. The lateral fibres of M.ptyerygoideus dorsalis have a substantial area of insertion on the medial surface of the mandible, anterior to the base of the internal process, and the insertion of M.pter.vent.lat. includes a well developed venter externus. The posterior region of M.pter.dors.med. and the medial region of M.pter.vent.med. are modified to form a large retractor palatini portion, with substantial fleshy attachment on the basitemporal plate. The retractor palatini fibres arise partly on the medial half of the ventral surface and

on the medial crest of the palatine; and also on the postero-medial edge (including part of the dorsal surface) of the pterygoid. The part arising on the pterygoid is bulky, and is prominent in dorsal view. The lateral half of M. pter. vent. med. is of normal structure, arising mainly on the lateral half of the ventral surface of the palatine, and inserted on the internal process of the mandible, with a raphe (Ap. N) fanning out from the medial tip of the internal process.

PHOENICULIDAE. *Phoeniculus purpureus*. As in *Upupa*, there is no separation of lateral and medial parts of M. pter. dors. This muscle is, however, strongly bipinnate, the raphe running in its outer quarter, roughly parallel to its lateral edge. The raphe is continuous medially with Ap. N, and dorsally with Ap. M. Ap. N. has an extended region of attachment to the mandible in the form of a crista along the dorsal edge of the anterior face of the internal process. The origin of M. pterygoideus dorsalis extends a long way forward, and its anterior edge is attached fleshily and by a dorsal aponeurosis to the whole ventral edge of the maxillo-palatine. M. pter. vent. med. also has a long area of origin on the ventral surface of the palatines, and there is a thin superficial band of fibres running from the groove between M. pter. vent. med. and M. retractor palatini to the mucosa in the midline. (Fig. 9c, ptvms). Other features, including the structure of M. retractor palatini, resemble *Upupa epops*. *P. aterrimus* resembles *P. purpureus*, but M. pter. dors. is not bipinnate, though attached to the maxillo-palatine. The venter externus is bulky, with a strong lateral aponeurosis which has a group of fibres attached in unipinnate fashion along its dorsal edge. *Rhinopomastus cyanomelas* shows attachment of M. pter. dors. to the maxillo-palatine, but as in *P. aterrimus*, the muscle lacks bipinnate structure. The venter externus is rather weaker than in the two previous species, with no obvious lateral aponeurosis or pinnate structure.

BUCEROTIDAE. *Tockus erythrorhynchus*. M. pterygoideus dorsalis is divided into lateral and medial parts by a clear groove running at approx. 40° to the midline of the skull. The pterygoid ramus of the Vth cranial nerve enters M. pter. dors. med. some way posterior to the groove, rather than passing into the groove itself as in all other birds considered in this study (except those showing no separation of medial and lateral parts). M. pter. dors. med. has an origin confined to the anterior edge of the pterygoid, but the retractor palatini portion of the muscle has an extensive dorsal origin including not only the posterior edge of the pterygoid, but also the medial edge of the posterior end of the pterygoid. The retractor palatini is pinnate in structure, with the raphe arising on the posterior tip of the palatine. The raphe is visible on the lateral face of the dorsal attachment of the muscle, fibres dorsal to it running more or less parallel with it, while those ventral to it diverge forwards to attach on the pterygoid.

M. pter. dors. lat. is weakly bipinnate about a broad dorsal aponeurosis (Ap. M.). Anteriorly there is an extensive fleshy origin along the whole length of the maxillo-palatine. M. pter. vent. lat. has an extremely bulky venter externus, bulging out prominently on the lateral surface of the mandible. M. pter. vent. med., apart from the retractor palatini portion, is of normal structure, with a strong raphe (Ap. N).

PICIFORMES

The main departures from the general description are seen in the Galbulidae, in which M. pterygoideus lateralis shows extreme reduction; and in the Capitonidae and Ramphastidae, in which attachment of M. pter. dors. lat. to the maxillo-palatine is found.

GALBULIDAE. *Galbula dea*. M. pter. dors. lat. and M. pter. vent. lat. form a single unit which is greatly reduced in size by comparison with other birds. It consists of a narrow slip originating via Ap. A1 along the lateral edge of the palatine, and inserted on the ventro-medial and ventral edge of the mandible at the base of the internal process. In dorsal view, the groove separating M. pter. lat. from M. pter. dors. med. is oriented at the very narrow angle of 10° to the midline of the skull. M. pter. dors. med. extends appreciably further forward on the palatine than M. pter. lat. The pterygoid ramus of the Vth cranial nerve enters the muscle through

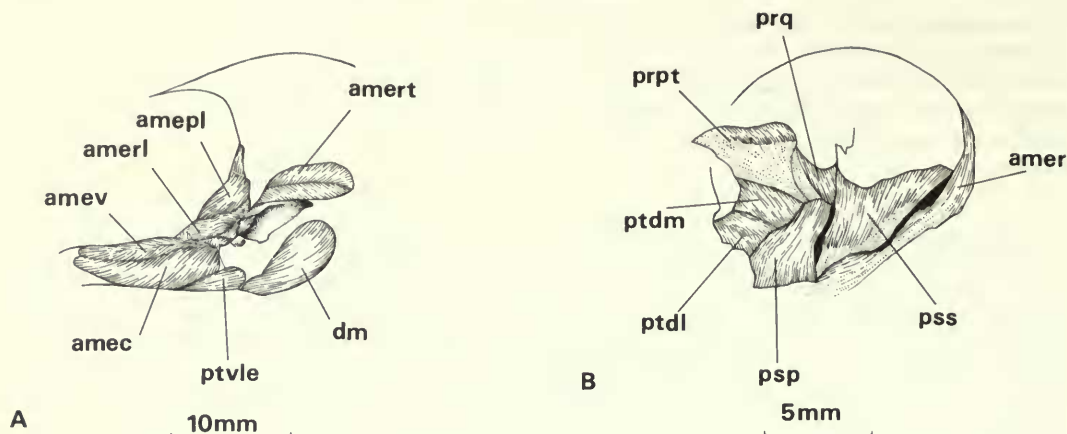


Fig. 24 *Dendrocopos major*, jaw musculature: A, lateral view; B, dorsal view.

the groove near the orbital process of the quadrate in the normal way. The remainder of the muscle is of normal structure.

In *Jacamerops aurea* there is a partial groove extending across the antero-medial half of the M. pter. dors. med. well back, and oriented at approx. 30° to the skull midline. M. pter. lat. is least reduced in *Galbalcyrhynchus leucotis*, in which the groove separating it from M. pter. dors. med. is angled at 15° to the midline.

BUCCONIDAE. *Chelidoptera tenebrosa*. M. pterygoideus dorsalis is of normal structure, with the groove separating lateral and medial parts situated well back, and angled at 45° to the skull midline. M. pter. dors. med. extends only onto the posterior end of the palatine. Ventrally, M. pter. vent. med. shows marked separation between fibres originating on the main ventral surface of the palatine, and those originating on the medial crest, which pass superficial to the main part of the muscle. M. pter. dor. lat. inserts low, on the ventral edge of the mandible. The venter externus is very small.

In all other Bucconidae examined, M. pterygoideus dorsalis shows an approach to the Galbulidae, with M. pter. dors. med. extending further onto the palatine, and the groove separating it from M. pter. dors. lat. oriented much more parallel to the skull midline than in Chelidoptera. In most species, the groove is noticeably curved, its posterior quarter or so being more steeply angled to the midline than the rest. Extremes are reached in *Notharcus macrorhynchus* and *N. tectus*, and in *Nonnula ruficapilla*, in which the angle of the groove to the midline is approx 20° over most of its length, and M. pter. dors. med. reaches the antero-dorsal crest of the palatine, and is noticeably larger than M. pter. dors. lat. Less extreme angles, and smaller extensions of M. pter. dors. med. onto the palatine are seen in, e.g. *Hypnelus ruficollis* (approx. 30°), *Malacoptila panamensis* (27°), *Monasa morphoeus* (26°), *Nystalus chacuru* (25°). In *Nystalus chacuru*, *N. radiatus* and *N. maculatus*, M. pter. dors. lat. is weakly bipinnate about a broad dorsal aponeurosis derived from Ap. M. The venter externus is weakly developed throughout, and entirely absent in *Hypnelus ruficollis* and *Nonnula ruficapilla*.

CAPITONIDAE. *Megalaima haemacephala*. M. pter. dors. med. is very narrow, and situated far back, its boundary with M. pter. dors. lat. angled at 55° to the skull midline. Its origin nevertheless includes substantial attachment to the posterior end of the palatine. M. pter. dors. lat. is of simple structure, but its anterior end has attachment, fleshily and by a short, weak dorsal aponeurosis, to the medial 2/3 of the ventral edge of the maxillo-palatine. There is no venter externus. M. pter. vent. med. is of normal structure.

In most other barbets examined, M. pter. dors. med. is relatively larger, and extends further

forward, the angle to the midline of its boundary with M.pter.dors.lat. ranging from 45° (*Trachyphonus vaillantii*) to 35° (*Pogoniulus leucolaima*, *Gymnobucco pelli*).

The extent and mode of attachment to the maxillo-palatine shows interesting variation. No attachment was found in *Psilopogon pyrrholophus*, *Gymnobucco pelli*, *Trachyphonus vaillantii* or *Capito niger*. In *Lybius bidentatus* there is a small amount of attachment on the ventral surface of the maxillo-palatine. In *Megalaima virens* there is a distinct attachment, but occupying rather less of the maxillo-palatine than in *M. haemacephala*. In *Pogoniulus leucolaima* the attachment is made by a distinct, if narrow, dorsal slip. The attachment is best developed in *Semnornis frantzii* and *S. ramphastinus*. In both species there is a distinct and well developed dorsal slip attaching on the medial half of the ventral edge of the maxillopalatine, fleshily and by a strong dorsal aponeurosis. Lateral to the slip, the origin of the muscle extends onto the dorsal surface of the palatal mucosa, near the rictus. In *S. ramphastinus* there is a narrow band of fibres lateral to Ap. M and diverging forward from it in unipinnate fashion.

INDICATORIDAE. *Indicator indicator*. M. pterygoideus shows no unusual modifications, although extending well forward on the dorsal surface of the palatine, there is no attachment to the maxillo-palatine. M.pter.dors. is clearly divided into lateral and medial portions by a groove running at approx. 47° to the skull midline. The origin of M.pter.dors.med. is confined to the pterygoid (see p. 355 regarding structure of the pterygo-palatine junction in this family and the Picidae). M.pter.dors.lat. is bipinnate, with the raphe in the lateral fifth or quarter of the muscle. M.pter.vent.lat. and med. are of normal structure, and there is no venter externus. M.pter.dors.lat. is scarcely bipinnate in *I. maculatus*, and not all in *I. minor*. *Melichneutes* resembles *I. indicator*.

RAMPHASTIDAE. *Selenidera maculirostris*. M.pter.dors.med. is narrow, and situated well back, its boundary with M.pter.dors.lat. oriented at 45° to the skull midline. M.pter.dors.lat. itself has an extensive attachment to the whole ventral edge of the maxillo-palatine in addition to its origin on the palatine. This attachment is made by a bulky raised dorsal slip, fleshily, and by a strong dorsal aponeurosis. The slip overlaps the lateral part of the palatine origin on its medial side. Beneath it lies a separate thin sheet of fibres with origin on the dorsal surface of the mucosa round the rictus, fleshily, and by a ventral aponeurosis (an extension of Ap. A1). There is scarcely any development of a venter externus. The rest of the muscle is of normal structure. *Ramphastos toco* is similar, but the slip originating on the maxillo-palatine is relatively even broader. The groove separating lateral and medial parts of M.pter.dors. is absent.

PICIDAE. *Jynx torquilla*. M.pter.dors.med. is narrow, and separated by a gap of about 10° from M.pter.dors.lat. The midline of this gap is oriented at about 65° to the skull midline. The origin of M.pter.dors.med. is confined to the pterygoid. Otherwise, the muscle shows no unusual modifications, and M.pter.dors.lat. is of simple structure. M.pter.vent.lat. and med. are of normal structure; there is no venter externus. *Dendrocopos major* has a strikingly elongated M.pter.dors.lat., extending forward almost to the midpoint of the nostril. This has a narrow band of fibres lateral to Ap.M., diverging forwards in a unipinnate arrangement. It is separated by a groove oriented at 40° to the skull midline from M.pter.dors.med., which has its origin confined to the pterygoid. There is no maxillo-palatine attachment or other unusual features. M.pter.vent.lat. and med. are of normal structure, and there is a moderately developed venter externus. Other woodpeckers examined are similar. In *Picumnus olivaceus* M.pter.dors.lat. is somewhat shorter, and of simple structure; otherwise, M.pterygoideus resembles that of the Picinae.

M. protractor pterygoidei et quadrati.

This muscle originates from the interorbital septum and the posterior wall of the orbit, medial to M. pseudotemporalis superficialis. Its insertion is on the dorsal surface of the posterior end of the pterygoid, and on at least the region of the quadrate body immediately

adjacent to the pterygoid; there is frequently also insertion on the postero-medial surface of the orbital process. In some birds, the regions of the muscle originating on the interorbital septum and the posterior orbit respectively show more or less differentiation into two distinct parts. In such cases, the part originating on the septum is referred to as 'M. protractor 1', and that arising on the posterior orbit as 'M. protractor 2'. The insertion of M. protractor 1 is a narrow one on the dorso-medial surface of the posterior end of the pterygoid, and is partly made via an aponeurosis; that of M. protractor 2 is wider and fleshy, on the quadrate body and usually also the postero-medial surface of the orbital process. The lateral fibres of M. protractor 2 may pass dorsal to the insertion of M. protractor 1. Medial fibres of M. protractor 2 may attach on the aponeurosis of M. protractor 1 in a pinnate arrangement.

ALCEDINIDAE. The muscle is narrow in form, but relatively fairly large. It shows no differentiation into parts 1 and 2, and has no attachment to the orbital process, which is in any case vestigial or absent in the Alcedininae and several Cerylinae.

TODIDAE. M. protractor is well developed, and its origin on the orbitum and interorbital septum is high. It shows slight differentiation into two parts, but there is only limited attachment to the orbital process, low down, near its base.

MOMOTIDAE. M. protractor is narrow, its origin extending high on the orbit and interorbital septum. It has no attachment to the orbital process. In *Baryphthengus* it shows slight bipinnate structure, but there is no real differentiation into two parts.

MEROPIDAE. M. protractor is large, and has insertion over the entire medial surface of the orbital process. However, it shows no differentiation into two parts.

LEPTOSOMATIDAE. The muscle is relatively rather small, but has extensive attachment to the orbital process. There is no clear division into two parts.

CORACIIDAE. M. protractor is relatively small. It has attachment to the postero-lateral half of the orbital process, but shows no differentiation.

UPUPIDAE. M. protractor is extremely large, its origin extending high, and nearly to the anterior end of the orbit. It is differentiated into two parts; part 1 is surrounded near its insertion by a strong aponeurosis, which is strongest along the posterior edge and partly ossified in some specimens. Fibres of part 1 run ventrally and posteriorly to their attachment on this aponeurosis, and fibres of part 2 run ventrally and anteriorly to attach to its other side in a strongly bipinnate arrangement. There is, however, no attachment to the orbital process.

PHOENICULIDAE. Similar to Upupa, but part 1 extends rather less far forward, especially in *Rhinopomastus*. Parts 1 and 2 are even further differentiated in *Rhinopomastus*, lateral fibres of Part 2 passing across the dorsal side of Part 1 at its insertion, but as in *Phoeniculus*, there is no attachment to the orbital process.

BUCEROTIDAE. M. protractor is quite small, and shows no differentiation or attachment to the orbital process.

GALBULIDAE. The muscle is fairly large, but generally of simple structure; there is an indication of differentiation into two parts in *Galbalcyrhynchus* and *Jacameros*. There is attachment to the full length of the orbital process.

BUCCONIDAE. The development of M. protractor varies considerably. It appears to be best developed in *Hypnelus bicinctus*, in which the origin extends high on the interorbital septum, and there is a distinct division into parts 1 and 2. Part 2 is attached over most of the orbital process except the medial half of its medial edge. It is attached to the entire medial surface of the orbital process in *Nonnula ruficapilla*, although there is no differentiation into two parts. It is well developed also in *Chelidoptera*, and somewhat less so in *Nystalus*. In *Notharcus*, *Malacoptila* and *Monasa*, M. protractor is relatively small, and has little attachment on the orbital process.

CAPITONIDAE. *M. protractor* is generally narrow, and of simple structure, with no attachment to the orbital process. In *Psilopogon*, its aponeurosis appears particularly well developed along its anterior edge, and fibres insert on it in unipinnate fashion.

Indicatoridae. Very similar to most Capitonidae.

RAMPHASTIDAE. Similar to the Capitonidae.

PICIDAE. In *Jynx*. *M. protractor* resembles that of the Capitonidae. It is narrow and fairly small, with no subdivision or attachment to the orbital process. In the remaining members of the family, including *Picumnus*, the muscle is greatly enlarged, and clearly divided into two parts, and attached to the entire medial surface of the orbital process. Part 1 attaches high and far forward on the interorbital septum. Its insertion is by a very strong aponeurosis arising from a long spur on the pterygoid. Part 2 arises from the posterior orbital wall; some of its medial fibres insert on the aponeurosis of Part 1, but most on the orbital process. In some, the area for insertion is slightly increased by a small aponeurosis extending medially from the tip of the orbital process, and merging with the aponeurosis of Part 1.

M. depressor mandibulae

This muscle is fairly small, and of uniform structure throughout the species examined, with the exception of the Upupidae and Phoeniculidae. In general, it originates from the exoccipital and inserts over a wide area on the posterior end of the articular, including the posterior surface of the internal process of the mandible. Both origin and insertion are mainly fleshy. In the birds examined here, surface aponeuroses are in most cases only moderately or weakly developed. They occur on the dorsal surface of the muscle (arising from the ventral edge of the exoccipital) and near the insertion, on the lateral and central surfaces (arising from the lateral and ventral edges of the posterior face of the articular).

In the Upupidae and Phoeniculidae, the muscle is much larger than in the other families studied, extending at the origin well up onto the temporal region of the squamosal. The area for insertion is increased by the development of a long retroarticular process—a backward extension of the articular, continued some distance posterior to the internal process. Only the medial face of the retroarticular process is occupied by *M. depressor*, whose fibres run rostro-lateral to meet it. Lateral and dorsal aponeuroses are well developed, but show no infolding or internal branches as in, e.g. the Huia (Callaeidae, *Heteralocha acutirostris*; see Burton 1974b) and some Charadrii (Burton 1974a). However, in the Phoeniculidae, some ventral fibres pass under the edge of the lateral aponeurosis and insert in a narrow band along the ventral border of its lateral surface. The only other family showing any approach to the Upupidae and Phoeniculidae is the Bucerotidae. In this family, although the muscle shows no marked enlargement, there is a definite indication of a retroarticular process, the postero-ventral corner of the articular projecting backwards, rather than being emarginated as in all the remaining families.

Tongue and hyoid apparatus

Although the morphology of the horny tongue has been described for a number of Coraciiform and Piciform birds (e.g. in Beddard, 1898), anatomical details of the hyoid skeleton and musculature are largely lacking, except in the case of the Picidae (Leiber, 1907a & b). Nomenclature used in descriptions largely follows that of Bock (1972) and Richards & Bock (1973) N.A.A. equivalents (Baumel *et al.* 1979) are given where they differ from terms used here.

Tongue

The horny tongue varies greatly among the families studied. Extreme tongue reduction is seen in the Alcedinidae, Upupidae, Phoeniculidae and Bucerotidae. Very long tongues are

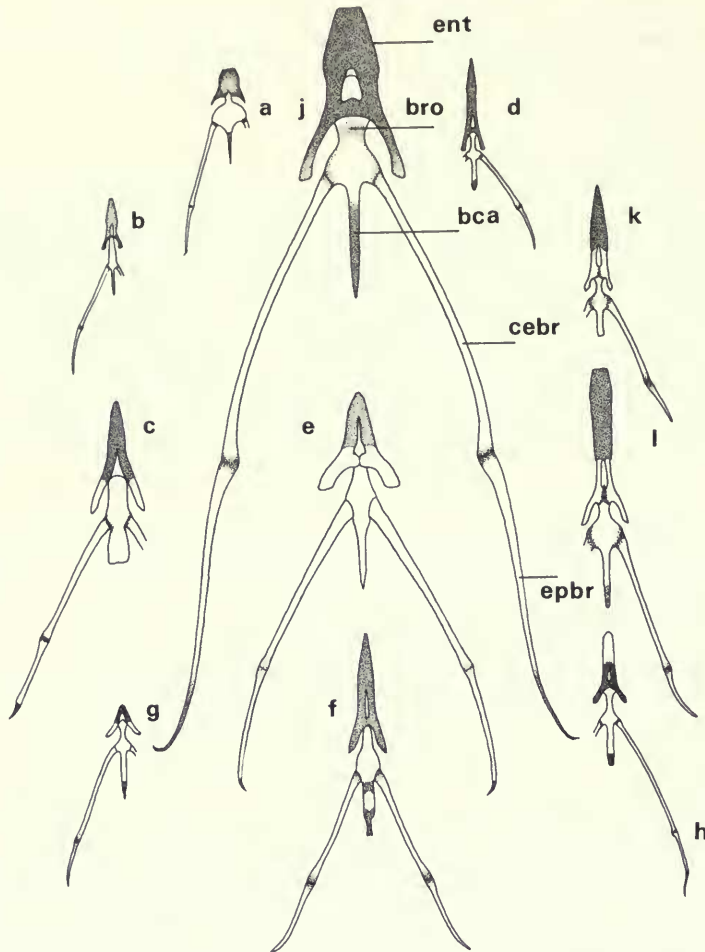


Fig. 25 Hyoid skeletons of Coraciiformes and Galbuloidea. Cartilage revealed by bulk staining with New Methylene Blue is indicated by stippling. (a) *Alcedo atthis*; (b) *Todus todus*; (c) *Momotus momota*; (d) *Aerops albicollis*; (e) *Leptosomus discolor*; (f) *Coracias benghalensis*; (g) *Upupa epops*; (h) *Phoeniculus purpureus*; (j) *Buceros bicornis*; (k) *Galbula dea*; (l) *Monasa morphoeus*.

seen in several families, such as the Coraciidae (particularly the ground rollers), Momotidae, a few barbets and the Ramphastidae. In absolute values, the tongues of the larger toucans must rank among the longest of all birds.

The extraordinarily long and extensible tongues of the Picidae cannot be directly compared with those of other families, since much of their length is taken up by the greatly elongated basihyal, and part of the hyoid horns; the horny tongue itself is much reduced, though still a vital part of the feeding apparatus. Surveys of the varied morphology of woodpecker tongues and hyoid apparatus have been provided by Steinbacher (1934, 1935, 1941, 1955, 1957).

Brush tongues occur in several families. Brush structure is highly developed, involving both tip and more or less of the sides in most Momotidae and the Ramphastidae. The latter family show this feature in extreme form; the tongue of *Ramphastos toco*, for example is a remarkable and beautiful structure, delicately tipped and fringed with fine laciniae for 80% of its considerable length. The Coraciidae, especially the ground rollers, also have quite well

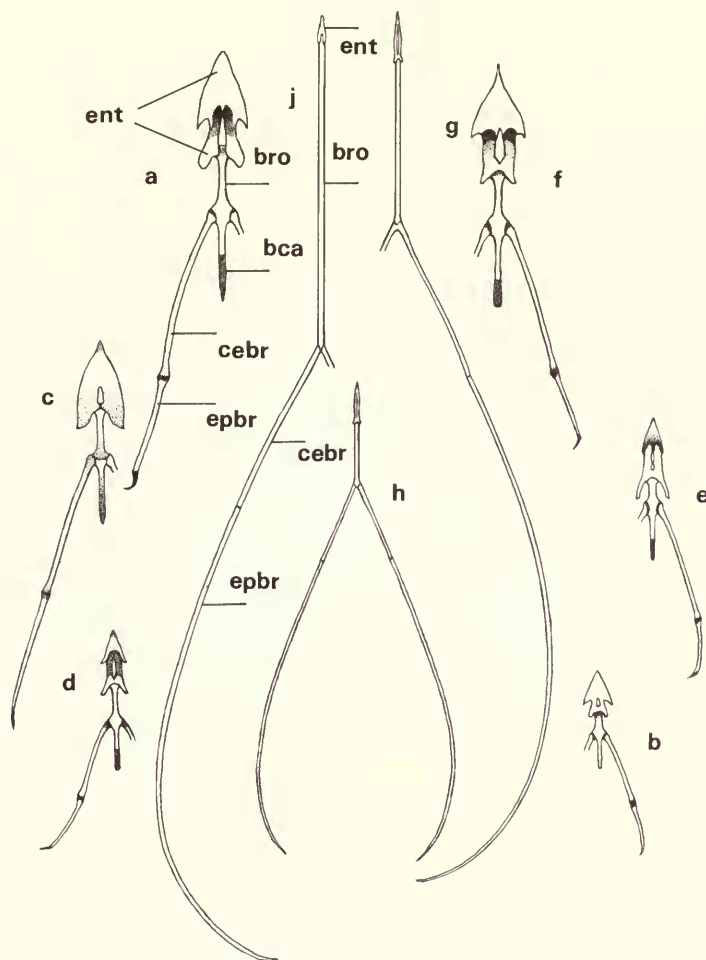


Fig. 26 Hyoid skeletons of Piciformes other than Galbuloidea. (a) *Psilopogon pyrolophus*; (b) *Pogoniulus bilineatus*; (c) *Lybius bidentatus*; (d) *Trachyphonus darnaudii*; (e) *Indicator indicator*; (f) *Selenidera maculirostris*; (g) *Jynx torquilla*; (h) *Sasia abnormis*; (j) *Colaptes auratus*.

developed brush tongues, and a moderate brush tip is also seen in *Capito* and *Semnornis* among the Capitonidae. Slight indications of brush structure at the tongue tip are seen in the Meropidae and *Jacamerops*. An African barbet (*Buccanodon melanolophus*) has a bifid tongue tip. Barbed tongues are characteristic of Picidae other than *Jynx*.

Apart from these, tongues are of simple structure for most of their length in all other species, that is to say, in the Alcedinidae, Todidae, Upupidae, Phoeniculidae, Bucerotidae, Bucconidae, Indicatoridae and most Galbulidae and Capitonidae. Basal barbs are normal as in most birds, but are particularly numerous in the Phoeniculidae and Bucerotidae, occurring on the dorsal surface as well as the margins in *Phoeniculus purpureus* and hornbills. Basal barbs are lacking in the Coraciidae, as noted by Beddard (1898). Many species show a slight indication of a median groove dorsally, corresponding with a ridge on the horny lining of the upper jaw, but a particularly strongly marked groove is characteristic of the Bucconidae, and quite noticeable also in *Jacamerops* and *Galbula* (Galbulidae).

Hyoid skeleton

The hyoid skeletons of representative species of each family are depicted in Figs. 19 & 20.

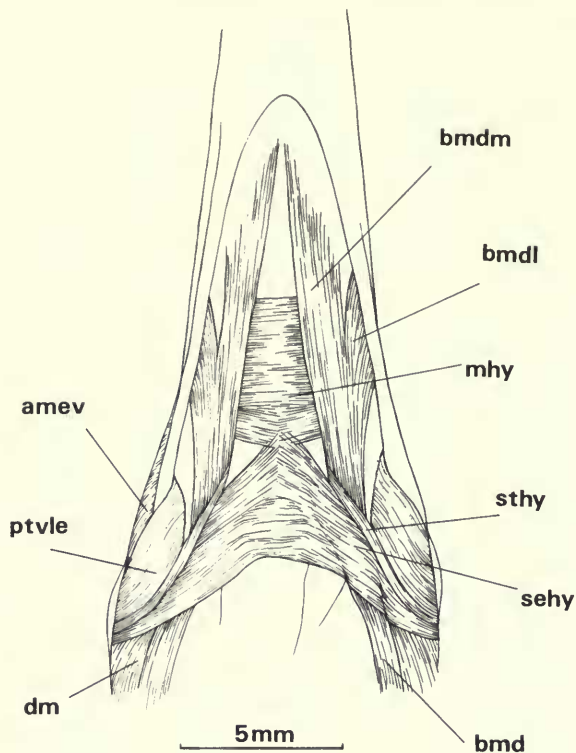


Fig. 27 *Todus todus*. Ventral view of superficial tongue muscles.

These illustrations eliminate much of the need for description; however, a few points deserve comment. The entoglossum generally tends to be more heavily ossified in the Piciformes than in the Coraciiformes, where any ossification is mainly confined to its posterior half. In general, the postero-lateral processes are longer in the Coraciiformes, producing more of an 'arrowhead' shape than in the Piciformes. The size of the entoglossum generally reflects the development of the tongue, but its form shows various features of interest in some Piciformes. The peculiar broadened tip of the entoglossum in *Monasa* is perhaps of minor significance; its sharply demarcated cartilaginous anterior and bony posterior much resemble the entoglossum of *Galbula*. Among the typical Piciformes, a more intriguing modification is seen; this takes the form of a strongly broadened anterior section, in some cases with backwardly directed lateral processes, as though an additional entoglossum had been grafted onto the front of the original. Of the Capitonidae checked for this feature, *Psilopogon* and *Trachyphonus darnaudii* showed it in a strongly developed form, and *Megalaima virens* moderately, while it was absent in *Lybius bidentatus*. Among other families, it is strongly developed in *Selenidera*, and moderately in *Indicator*. Within the Picidae, the entoglossum is very short and narrow, though with a slightly narrowed 'waist' posteriorly in *Jynx* and *Sasia*.

The basihyal is rather short and often broad in most Coraciiformes, and in the Galbulidae and Bucconidae. Broadening reaches an extreme in the Alcedinidae, where the basihyal is broader than long, forming a flat plate, with just a tiny narrow projection anteriorly to articulate with the entoglossom. The basihyal has well marked lateral flanges in the Todidae. In the Upupidae and Phoeniculidae, the basihyal has a characteristic 'hour-glass' form, also seen, though less strongly, in the Bucerotidae. In the typical Piciformes, the basihyal is

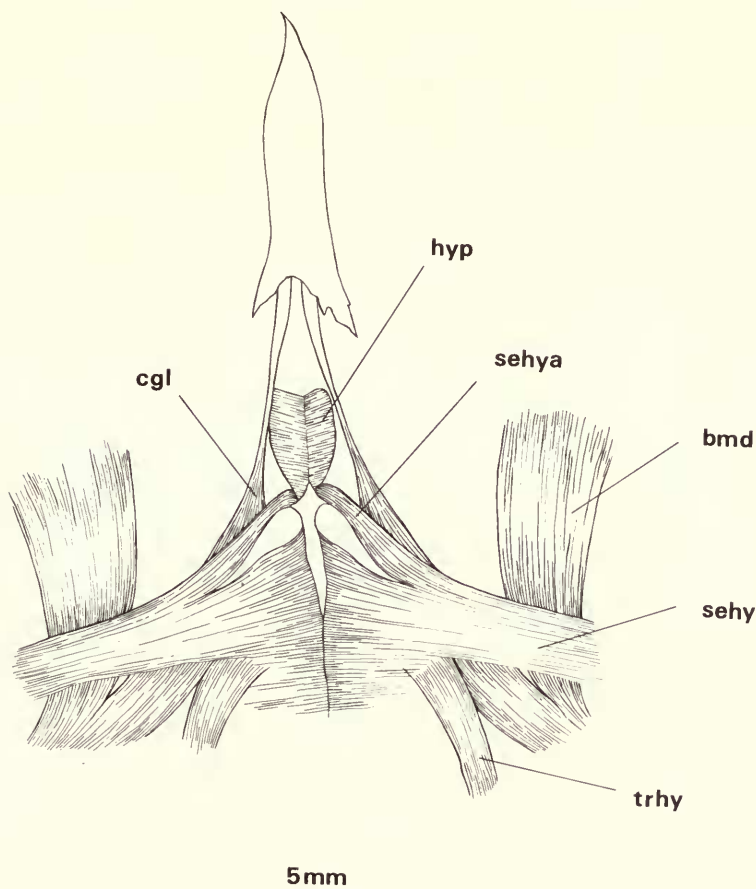


Fig. 28 *Coracias abyssinica*. Ventral view of tongue muscles to show anterior slip of *M. serpihyoideus*.

generally simple in shape, and rather long and narrow, reaching an extreme in the Picidae. *Pogoniulus* and *Indicator* are exceptions in which the basihyal is rather short.

Other parts of the hyoid skeleton require little comment. It may be noted that the great length of the hyoid horns seen in the Picidae has been attained mainly by elongation of the epibranchiale.

Hyoid muscles

M. mylohyoideus (N.A.A.: *M. intermandibularis*)

This very thin muscle is a sheet of fibres extending across the floor of the buccal cavity between the medial surfaces of the two mandibular rami, to each of which it is attached fleshily along a narrow line dorsal to *M. branchio-mandibularis* (and *M. genioglossus* where present). Its posterior end may merge with *M. serpihyoideus*. There appears to be no median raphe of insertion as in *Loxops* (Richards & Bock, 1973). The muscle is weakly developed in most of the families examined here, and was barely detectable in *Coracias benghalensis*, *Galbula dea* and *Megalaima haemacephala*. It appeared best developed in the Meropidae, *Indicator* and the larger Capitonidae. However, comparisons are rendered difficult by the varying states of contraction of the muscle in different specimens, resulting from the common practice of putting cotton wool plugs into the buccal cavity of specimens at the time of collection.

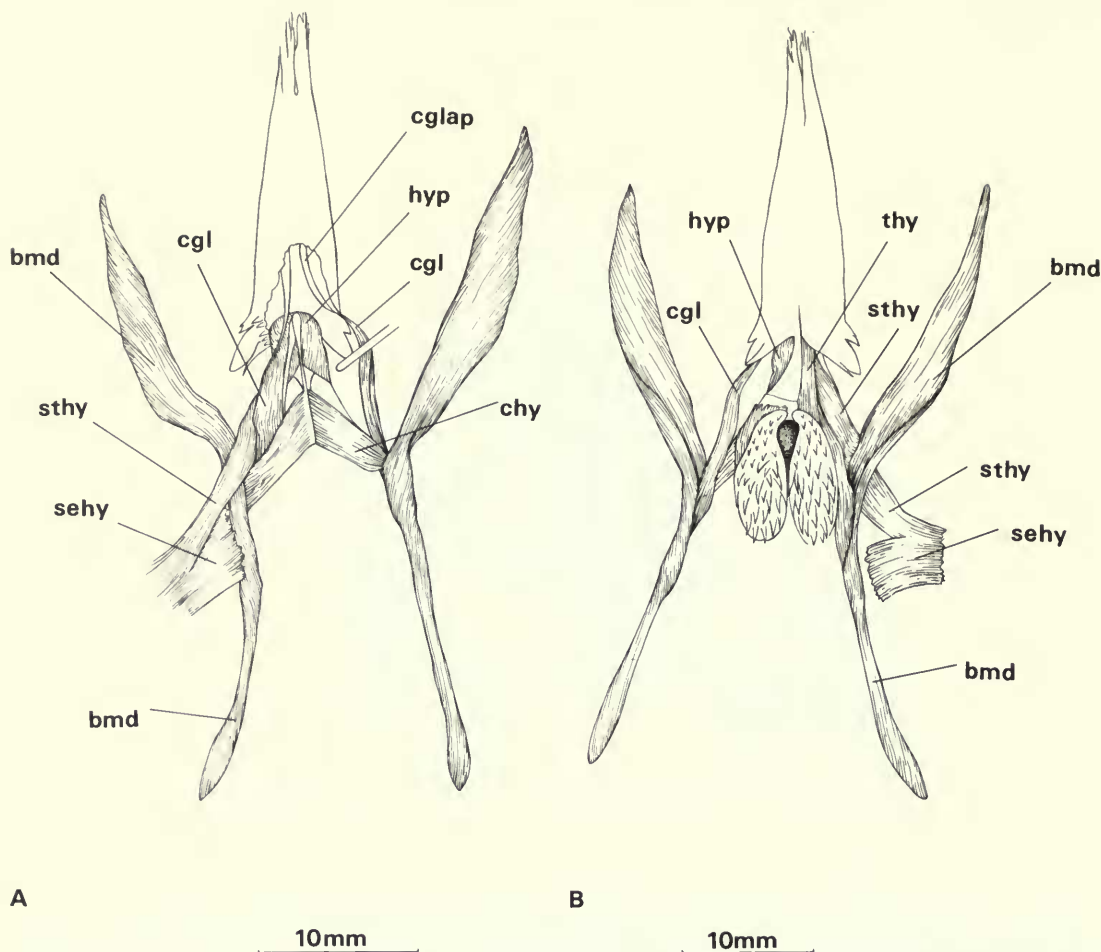


Fig. 29 *Megalaima zeylanica*, tongue musculature: A, ventral view; B, dorsal view. Left M. ceratoglossus free from basihyal and pinned aside.

M. ceratohyoideus (N.A.A.: *M. interceratobranchialis*)

The muscle originates fleshily on the ceratobranchiale close to its articulation with the epibranchiale. It passes along the ceratobranchiale, surrounded by *M. branchiomandibularis*, then diverges medially to insert on a median raphe with *M. ceratohyoideus* from the opposite side. The insertion lies deep to *M. serpihyoideus* and *M. mylohyoideus*, and immediately ventral to the urohyal.

M. ceratohyoideus is absent in the Indicatoridae and Picidae, and feebly developed in the Alcedininae, in which insertion is on the posterior edge of the basihyal and anterior tip of the urohyal, rather than on the midline. Otherwise it shows little noteworthy variation among the species studied.

M. stylohyoideus

This muscle has a common fleshy origin with *M. serpihyoideus* on the postero-ventral edge of the mandible. It appears as a narrow slip which diverges from the anterior edge of *M. serpihyoideus* and runs to a fleshy insertion on the dorso-lateral surface of the basihyal, typically at its anterior end, and lateral to that of *M. thyrohyoideus*. This is its condition in the families studied here, with the following exceptions:

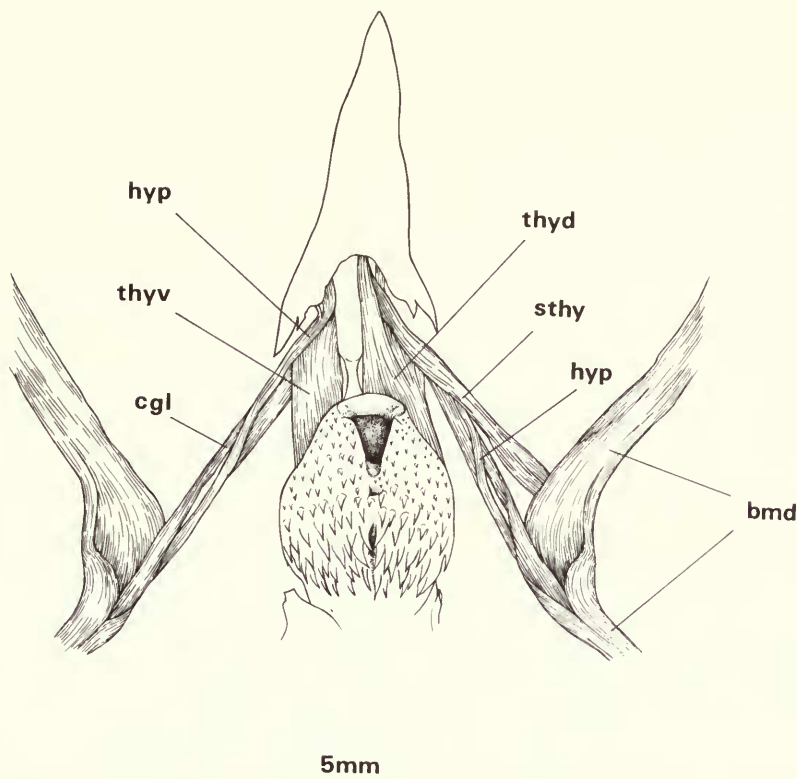


Fig. 30 *Indicator maculatus*. Dorsal view of tongue musculature to show *M. hypoglossus obliquus*.

ALCEDINIDAE. Insertion is on the dorsal surface of the anterior tip of the ceratobranchiale.

TODIDAE. *M. stylohyoideus* is extremely slender and absent in one specimen.

MOMOTIDAE. Insertion on the dorso-lateral surface of the posterior end of the basihyal.

CORACIIDAE, Galbulidae, Bucconidae: *M. stylohyoideus* is apparently replaced by a slip from *M. serpihyoideus* (q.v.).

UPUPIDAE. Extremely slender.

BUCEROTIDAE. Absent.

PICIDAE. Generally much reduced, with no attachment on the hyoid skeleton, and probably absent in some (see Leiber, 1907*a* & *b*).

M. serpihyoideus

Origin is on the postero-ventral edge of the mandible, medial to that of *M. stylohyoideus*. The insertion is on a medial raphe, the right and left muscles together forming a shallow, forwardly directed 'V'. The anterior tip is in close proximity to *M. mylohyoideus* posterior, and may merge with it. The muscle is similar in all the groups examined except the Coraciidae, Leptosomatidae, Galbulidae and Bucconidae. In these families, a narrow slip diverges from the anterior edge of the muscle (which is very narrow in *Leptosomus*) to insert around the ceratobranchiale-basihyal articulation. The insertion is in fact on the ventral surface of the anterior tip of the ceratobranchiale in all except *Eurystomus* and *Leptosomus*, in which attachment is on either side of the posterior ventral surface of the basihyal. Where *M. stylohyoideus* is absent (Coraciidae, Galbulidae, Bucconidae) this slip corresponds with it in origin, but is quite distinct in its completely ventral insertion, rather than a lateral or dorsal

one. However, the presence of both this slip and a normal *M. stylohyoideus* in *Leptosomus* makes it clear that the slip is not just a *M. stylohyoideus* with altered insertion.

M. branchiomandibularis

In all birds previously studied, *M. branchiomandibularis* (= *M. geniohyoideus*) originates fleshily on the medial surface of the mandible just anterior to the venter externus of *M. pterygoideus ventralis medialis* (if present), and division at the origin into an anterior and a posterior portion is common. This is also its origin in some of the families investigated here, but a modified form of origin (either far anterior on the mandible, or from the ventral surface of the buccal mucosa) is seen in others. In this modified form, the muscle is flattened in the horizontal plane, whereas in its typical condition, flattening is less pronounced and oriented nearer to the vertical plane.

In all cases, insertion is fleshy on the distal part of the epibranchiale. The muscle is twisted around both ceratobranchiale and epibranchiale. *M. branchiomandibularis* is generally the largest tongue muscle, and in the Picidae reaches an enormous size due to the great elongation of the hyoid horns. Variations in the size and position of these horns are described by Steinbacher (1934 *et seq.*).

ALCEDINIDAE. *Alcedo*. Origin entirely on the medial surface of the mandible and extending far forward nearly to the mandibular symphysis. There is no clear division into two parts. The hyoid horns, and therefore the area of insertion, are short.

Other Alcedininae resemble *Alcedo*. In the Cerylinae, *Megaceryle* spp., *Chloroceryle amazona* and *C. inda* resemble *Alcedo*. *Chloroceryle americana* and *C. aenea* show great reduction of *M. branchiomandibularis*. The origin is limited to a small area on the ventral medial edge of the mandible, just anterior to the venter externus of *M. pterygoideus ventralis medialis*. In *C. aenea* the muscle is reduced to a tiny slip, and could almost be termed vestigial. In the majority of Daceloninae, origin on the mandible is limited to the anterior region near the symphysis, but there is additional origin from the ventral surface of the buccal mucosa. In these species, the origin of the muscle is flattened in the horizontal plane, rather than the more vertical one shown where the mandible is the main site of origin. In *Pelargopsis*, *Tanysiptera* and *Lacedo*, attachment appears to be mainly from the mandible, as in *Alcedo*; in *Halcyon saurophaga* it is almost entirely from the mucosa.

TODIDAE. In three specimens of *T. todus* the origin is divided into two clear parts. The bulkier part is attached partly on the medial surface of the mandible, but mainly on the mucosa, extending well anterior. The smaller part is a slip running close to the midline, left and right sides being in contact in some specimens. This medial slip resembles an *M. genioglossus*, but is distinguished by its insertion on the epibranchiale, to which it runs medially and dorsally relative to the main part. In a fourth specimen, the origin is undivided and confined to the mucosa.

MOMOTIDAE. *Momotus*. The origin of *M. branchiomandibularis* is not subdivided, and is mainly on the medial surface of the mandible, with a small amount of attachment to the mucosa anteriorly. The insertion is normal.

In *Baryphthengus*, the origin is roughly half from the mandible and half from the mucosa. In *Electron*, the mucosa is the main site of origin, with only a small amount of attachment to the mandible.

MEROPIDAE. Origin is largely on the mucosa, extending far anterior, with only a small area of attachment on the mandible. There is no obvious subdivision of the muscle.

LEPTOSOMATIDAE. The origin of *M. branchiomandibularis* is of typical form, confined to the medial surface of the mandible, and showing clear division into anterior and posterior portion.

CORACIIDAE. Origin mainly on the mucosa (entirely in *Coracias*), extending anteriorly nearly to the symphysis. No subdivision.

UPUPIDAE. Origin entirely on the mandible, but extending far anteriorly. No subdivision, and rather narrow.

PHOENICULIDAE. Similar to the Upupidae.

BUCEROTIDAE. Origin is from a bony ledge at the mandibular symphysis, and the muscle is narrow and flattened in the horizontal plane. In *Tockus erythrorhynchus*, the left and right muscles meet in the midline at the symphysis, lying superficial to the origin of *M. genioglossus*, which is also on this ledge. In *Buceros bicornis* and *Bucorvus leadbeateri*, the left and right muscles remain separate at the origin, and do not overlap *M. genioglossus*.

GALBULIDAE. Origin resembles that in the Bucerotidae, being mainly from a medially situated bony ledge at the mandibular symphysis, though with some attachment also to the mucosa. The left and right muscles do not quite meet at the midline, although there is no *M. genioglossus*. The gap is widest in *Galbalcyrrhynchus*. The muscle is narrow and horizontally flattened.

BUCCONIDAE. As in the Galbulidae, except that the narrow gap between right and left muscles is occupied by a well-developed *M. genioglossus*.

CAPITONIDAE. *M. branchiomandibularis* originates entirely from the medial surface of the mandible, and consists of a single portion.

INDICATORIDAE. As in the Capitonidae, but there is some subdivision into two portions.

RAMPHASTIDAE. As in the Capitonidae.

PICIDAE. Despite the enormous size of this muscle in the Picidae, its origin is basically a conventional one on the medial surface of the mandible, though extending from the anterior edge of *M. pterygoideus ventralis medialis* forward to the mandibular symphysis. *M. geniothyreoides* (Leiber 1907a & b) is apparently a derivative of *M. branchiomandibularis*, originating anteriorly on the medial surface of the mandible, dorsal to *M. branchiomandibularis*, and inserting on the dorsal surface of the trachea, just posterior to the larynx.

M. genioglossus

This muscle is absent from many groups of birds, and where present, is often difficult to detect. Its origin is fleshy, or by a short aponeurosis, from the medial surface of the mandible, at or near the symphysis, and it runs along the ventral side of the buccal mucosa to insert in the region of the tongue base. It runs adjacent to a vein, and where poorly developed could well be confused with it. This vein is apparently a branch of the mandibular vein (Hughes 1934), joining it near the posterior end of the lower jaw. The vein appears to be present on the right side only in most of the families studied (both sides in *Alcedo atthis*; left side only in *Halcyon chelicuti*), but could not be traced in many specimens.

M. genioglossus was found in eight of the fifteen families investigated here, as follows:

MOMOTIDAE. Vestigial, left and right sides originating close together on the mandibular symphysis. It fades out short of the tongue base.

MEROPIDAE. Similar to the Momotidae; best developed in *M. pusillus*.

CORACIIDAE. Present in *Brachypteracias* spp., *Attelornis* and *Uratelornis*, and quite well developed. The origin is on the mandibular symphysis, where the right and left muscles unite. Insertion is on the ventral side of the mucosa lateral to the tongue base.

UPUPIDAE. A single, slender median muscle arising at the symphysis, and fading out on the mucosa just short of the tongue base. The site of origin is the ventral surface of a well developed bony ledge, level with the dorsal edge of the mandible.

PHOENICULIDAE. Origin is by a short aponeurosis from the symphysis, on a less distinctly marked bony ledge than in the Upupidae. The muscle is better developed and the right and left muscles unite only near the origin. Insertion is on the mucosa near the base of the tongue.

BUCEROTIDAE. A single median muscle, but very well developed. Origin is at the symphysis, from a more or less well marked bony ledge, shared also by *M. geniohyoideus*,

which lies ventral (superficial) to *M. genioglossus* in *Tockus*, and lateral to it in *Bucorvus* and *Buceros*. Insertion is on mucosa near the tongue base in *Tockus*, but around the posterior end of the basihyale in *Bucorvus* and *Buceros*. The muscle is particularly bulky in *Bucorvus*.

BUCCONIDAE. Present throughout, left and right muscles having a combined origin on the symphysis, and insertion on the mucosa lateral to the tongue base.

RAMPHASTIDAE. A vestigial median genioglossus was found in *Selenidera*, with origin at the symphysis, but fading out on the mucosa short of the tongue base.

PICIDAE. *M. geniothyreoideus*, included here under *M. branchiomandibularis* could alternatively be a modified form of *M. genioglossus*—see discussion, p. 435.

M. ceratoglossus

In all birds so far studied, this muscle originates fleshily entirely on the dorso-lateral surface of the ceratobranchiale. It is a pinnate muscle whose short fibres insert on a lateral aponeurosis. This merges anteriorly into a strong tendon inserting on a tubercle on the ventral side of the posterior end of the paraglossale. The dorso-medial surface of the muscle is concave, to fit the ceratobranchiale.

In the families investigated here the extent of origin is the principal feature showing variation. The origin is from the entire length of the ceratobranchiale in the Todidae, Leptosomatidae, Coraciidae, Bucerotidae, Galbulidae, Bucconidae and Picidae. The muscle stops more or less short of the anterior tip of the ceratobranchiale in the Alcedinidae, Momotidae, Upupidae and Phoeniculidae. In the remaining families there is more or less attachment also to the basihyal. In the Indicatoridae there is a slight amount of attachment to the basihyal just at its articulation with the ceratobranchiale. In the Capitonidae, there is attachment along the entire ventro-lateral surface of the basihyal except in *Trachyphonus* (posterior half of basihyal and ceratobranchiale only) and in *Psilopogon* (origin only on ceratobranchiale). In the Ramphastidae, origin includes the full length of the basihyal.

M. ceratoglossus anterior and *M. hypoglossus medialis*

The small muscles at the base of the tongue have given rise to considerable confusion in the literature. The definitions followed here are those employed by Burton (1974a). *M. ceratoglossus anterior* is the name given to a small group of fibres arising from the tendon of *M. ceratoglossus* just before its attachment to the ventral surface of the paraglossale. These fibres insert partly on the entoglossum, but mainly on a strong median aponeurosis which runs the length of the ventral surface of the tongue. *M. hypoglossus medialis* is an unpaired median muscle arising on the anterior tip of the basihyal and inserting on the median aponeurosis.

Both muscles, together with their median aponeurosis, are absent in the majority of families studied here. *M. ceratoglossus anterior* is present in the Meropidae, in which it is very small, and the Leptosomatidae, in which it is well developed. In the Ramphastidae, fibres from the main part of the muscle extend onto the paraglossale, but there is no distinct *ceratoglossus anterior*, and no median aponeurosis. *M. hypoglossus medialis* is found in the Meropidae, Galbulidae and Bucconidae; it is well developed in the first, smaller in the second, and extremely small in the third.

M. hypoglossus obliquus

In all birds previously studied this muscle originates on or around the basihyale and inserts fleshily on the postero-lateral tip of the paraglossale. Two main forms occur; in Type 1 (Burton, 1974a), the right and left muscles merge in the midline, forming a continuous band of fibres which passes under the basihyale. In Type 2, the right and left muscles meet ventrally, but remain separate. In Type 1, the muscle is generally shorter than in Type 2, and confined to the anterior part of the basihyale.

Most of the Coraciiformes examined conform reasonably closely to one or other type. However, the Upupidae, Phoeniculidae and Piciformes (with the exception of the Galbulidae and Bucconidae) show a highly distinctive modification of Type 2, in which the right and

left sides are entirely separate not even meeting ventrally and originate far back on the basihyale or in some also on more or less of the ceratobranchiale. In this modified form, the muscle is long and narrow, reaching an extreme in the Indicatoridae and Picidae, with its fibres oriented at only a small angle to the basihyale. This contrasts with its normal form, which is short and stout, the fibres being oriented at a large angle to the basihyale—90° in the case of the more anterior fibres.

ALCEDINIDAE. The muscle is of Type 2, but rather poorly developed, so that right and left sides usually fail to meet at the ventral midline, and leave the anterior half of the short basihyale exposed.

TODIDAE. Reasonably well developed, and of Type 1, completely covering the anterior half of the basihyale.

MOMOTIDAE. Type 2, completely covering the short basihyale.

MEROPIDAE. Type 2, but short, covering slightly less than half of the rather long basihyale.

LEPTOSOMATIDAE. Type 2, but short and rather small, covering slightly over half the short basihyale.

CORACIIDAE. Type 2, the left and right sides just failing to meet, but otherwise covering all of the short basihyale.

UPUPIDAE. The left and right muscles are completely separate, originating on the posterior basihyale, and the head of the ceratobranchiale; however the muscle is narrow and its total bulk is small, the basihyale being short.

PHOENICULIDAE. The two sides are quite separate, and origin is on the posterior basihyale, and the ceratobranchiale anterior to the origin of *M. ceratoglossus*. The muscle is somewhat shorter in *Rhinopomastus* than in *Phoeniculus*.

BUCEROTIDAE. The muscle is vestigial. The right and left muscles are separated by a wide gap, and their origin is confined to the anterior half of the basihyale. *M. hypoglossus obliquus* is completely concealed by the anterior fibres of the bulky *M. ceratoglossus*.

GALBULIDAE. Type 2, covering the entire basihyale.

BUCCONIDAE. Type 2, covering the entire basihyale.

CAPITONIDAE. The muscle is of Type 2, but long and narrow, with origin well back on the posterior half of the basihyale. The origin extends onto the anterior tip of the ceratobranchiale in *Pogoniulus*.

INDICATORIDAE. The muscle is very extensively developed, its origin including the posterior basihyale and the entire dorsal surface of the ceratobranchiale as far as its articulation with the epibranchiale. The origin is medial and dorsal to that of *M. ceratoglossus*. Insertion is by a strong, narrow dorsal aponeurosis, which extends back some distance into the origin, acting as the raphe of a bipinnate fibre arrangement.

RAMPHASTIDAE. The muscle is long and narrow, with an extensive origin on the posterior basihyale and anterior ceratobranchiale.

PICIDAE. From examination of *Jynx torquilla*, *Dendrocopos major* and *Picumnus olivaceus*, it seems quite clear that *M. ceratoglossus superior*, described by Leiber (1970a & b) in various Picidae, is in fact simply a very long *M. hypoglossus obliquus*. This point is considered in more detail in the discussion (pp. 417–418).

M. tracheohyoideus and *M. tracheolateralis* (N.A.A. terminology: see text)

These two muscles insert close together on the cricoid cartilage, and both run the length of the neck. *M. tracheohyoideus* arises on the sternum or clavicle, and runs lateral to *M. tracheolateralis*, adhering closely to the skin of the neck. *M. tracheolateralis* arises on the syrinx and runs along the ventro-lateral surface of the trachea.

The site of origin of *M. tracheohyoideus* is the clavicle in the Alcedinidae, Todidae, Momotidae, Meropidae, Leptosomatidae, Coraciidae, Upupidae, Phoeniculidae, Galbulidae and Bucconidae. The origin is usually a fairly wide fleshy one along a narrow line in the medial half or third of the anterior edge of the clavicle and right and left muscles remain

separate. The origin is fleshy on the antero-ventral tip of the keel of the sternum or the clavicular symphysis in the Capitonidae, Indicatoridae, Ramphastidae and Picidae. This is generally a narrower origin than that on the clavicle and right and left muscles meet at the origin. In the Bucerotidae, both sites of origin are utilized, and the muscle forms an extensive sheet over most of the ventral side of the neck, closely adhering to the skin.

In most of the families considered here, *M. tracheohyoideus* inserts fleshily on the medial surface of the ceratohyal, near its anterior end, and on the dorso-lateral surface of the cricoid between the two heads of origin of *M. thyrohyoideus*. In the Indicatoridae, attachment to the ceratohyal is slight, and in the Capitonidae (except *Psilopogon*) and Ramphastidae it is absent altogether. The complex insertions of *M. tracheohyoideus* in the Picidae are thoroughly described by Leiber (1907*a* & *b*).

(According to Baumel *et al.*, 1979 (N.A.A., *Systema respiratorium*, Note 45), the muscle originating on the clavicle should be called *M. cleidohyoideus* and that arising on the sternum should be *M. sternohyoideus*. However, the evidence of this study (particularly the condition in the Bucerotidae) seems to indicate that both are derived conditions of the same muscle, and the common term of *M. tracheohyoideus* for both has been given preference. See also Part 3, p. 418).

M. tracheolateralis inserts on the ventral surface of the cricoid, medial to the ventral origin of *M. thyrohyoideus*. It appears to be absent in *Coracias*. In the Upupidae, *M. tracheolateralis* merges with *M. tracheohyoideus*, and they insert together on the ventral cricoid and the anterior tip of the ceratohyal.

M. thyrohyoideus (N.A.A.: *M. cricohyoideus*)

This muscle originates from the cricoid cartilage by ventral and dorsal heads. The ventral head arises from the ventral surface of the cartilage, and the dorsal head from its lateral surface. Insertion is on the dorso-lateral surface of the anterior end of the basihyale—typically medial and slightly posterior to the insertion of *M. stylohyoideus* if present.

Little variation was encountered among the forms studied here.

The neck and its musculature

The most important general account of the avian neck is that by Boas (1929), providing the foundation for all subsequent studies. The account of passerine cervical anatomy by Palmgren (1949) is also of great value. Detailed studies of small groups of species have been made by Zusi (1962), Zusi & Storer (1969) and Burton (1974*b*). While this paper was nearing completion, a detailed account for several Picidae was published by Jenni (1981).

Cervical vertebrae

Despite the wide range of feeding apparatus modifications shown by the head in the two orders, the cervical vertebrae are relatively uniform in their major features. Defined as vertebrae which bear either no movable ribs, or movable ribs not articulating with the sternum, there are either fourteen or fifteen (Beddard, 1898). The cervical vertebrae of birds fall into three fairly well defined sections, with different functional properties (Boas, 1929). Section I (the most anterior) can only be flexed downward, Section II only upward, and Section III mainly downward, though anteriorly upwards as well. In the Coraciiformes and Piciformes, as in most birds studied, Section I usually consists of the first five vertebrae, 5 often appearing transitional, as in the Picidae; Boas (1929) gives a first section count of four for *Picus viridis*. Section II comprises vertebrae 6 to 9 or 10, and Section III the remainder. Descriptions of the morphological features which control the range of bending are given by Zusi & Storer (1969); although referring to a grebe (*Podilymbus*) possessing several more vertebrae than Coraciiform or Piciform birds, the structural modifications concerned are essentially similar.

Some noteworthy variations among the Coraciiformes and Piciformes may now be summarized. In Segment I, the first vertebra (the 'atlas') is, as in all birds, a simple ring of bone without a neural spine; in the Bucerotidae, it is fused with 2. Vertebrae 2 and 3 invariably

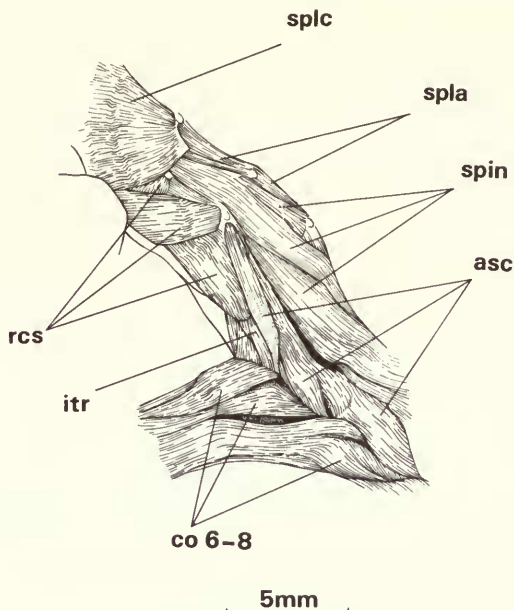


Fig. 31 *Alcedo atthis*. Superficial anterior cervical musculature. M. rectus capitis lateralis and ventralis and M. biventer cervicis not shown. M. complexus freed from cranium and turned aside.

bear tall neural spines, and so often, does 4. Neural spines are continued further back, in some cases, and extend to 6 or 7 in the Alcedinidae, Phoeniculidae, some Capitonidae and Picidae. The spines normally decrease evenly in height from front to back, though in some woodpeckers there is actually an increase from 2 to 4, and then a steady reduction in height. A series of fused ribs is generally present from 3 or 4 onwards (5 in *Leptosomus* and *Upupa*), but these are reduced in the Bucerotidae and absent in the Picidae. Some anterior vertebrae may possess bony struts connecting the transverse process with the dorso-lateral crest, or the costal process with the lateral crest, or both. Exactly which vertebrae varies widely; the dorsal strut occurs most commonly on 3 and 4, the ventral on 5, 6 and 7. Only two species examined (*Phoeniculus purpureus*, *Colaptes auratus*) had a dorsal strut on 2, and only two had ventral struts posterior to 7 (*Phoeniculus purpureus*, on 8; *Upupa epops* on 8, 9 and 10). Dorsal and ventral struts occur together, if at all, usually only on 4, but *Nystalus chacuru* is remarkable for having both together on 5, 6 and 7.

Hypapophyses occur anteriorly and posteriorly, but are absent from the middle region of the neck. The anterior ones are usually found on vertebrae 2 to 4, though often on 2 to 3 only. That on 2 is often distinctly bifurcate, the two projections pointing backwards. Those on 3 and 4 may have a similar, but less pronounced shape. In the Picinae, very deep hypapophyses are found on 2 to 5. The ventral side of the atlas (1) also bears a hypapophysis like process, which is frequently bifurcate posteriorly. This provides insertion for M. flexor colli brevis, and is particularly strongly developed in the Picinae. Posteriorly, hypapophyses extend back into the thoracic region, starting usually on 9 or 10, but on 8 in *Jynx*, 11 in *Nyctiornis*, *Upupa* and *Selenidera*, and on 12 in *Tockus*. In the Picidae (other than *Jynx*), the subvertebral bridge which is present from 5 or 6 rearwards shows some indication of a hypapophysis on all vertebrae, but this is only well defined on 10 (the last vertebra with such a bridge) and vertebrae posterior to it. The subvertebral bridge in the Picidae has long been known (see, e.g. Beddard, 1898), but has apparently not been noted in other Piciform families. However, there is a complete subvertebral bridge on 8 in *Indicator*, with an incomplete bridge also on 6, 7 and 9. In *Jynx*, a subvertebral bridge is present only on 8 and 9.

Cervical muscles

Dissection of neck muscles is arduous and time consuming, and it was found impractical to examine the full range of species used in other parts of this study. The species actually investigated are referred to in appropriate places in the text, and group names are used only where an adequate range of species has in fact been dissected. For similar reasons, three muscles (Mm. splenius accessorius, Mm. intercostales and Mm. interspinales) have been omitted, while for some others (M. longus colli ventralis, Mm. intertransversarii and Mm. inclusi) the level of detail studied has been deliberately limited.

M. biventer cervicis

Origin is from the dorsal aponeurosis of M. spinalis in the region of l3, and the muscle inserts on the dorsomedial edge of the occipital deep to M. complexus. As its name implies, this muscle has two fleshy bellies, at origin and insertion, while the middle region of the muscle consists of a flat strap like tendon. The length of this tendon relative to the fleshy bellies varies considerably. The muscle is best developed in the Alcedinidae, in which the muscle shows a further peculiarity first noticed by Cunningham (1870), in *Ceryle*. This is a short, strong aponeurosis linking the right and left muscles, near the posterior end of the anterior bellies. This feature was noted in various other kingfishers by Beddard (1896), and has been further checked in a wide range of other species for the present study. The transverse aponeurosis has been found throughout the Cerylinae, but in none of the Alcedininae examined. Within the Daceloninae, it was found in *Tanysiptera*, *Cittura* and *Halcyon sancta* (= *Sauroptatis vagans*) by Beddard, and in the present study also in *Melidora*; it is evidently absent in most, perhaps all, other members of the subfamily.

M. biventer is also well developed in the Indicatoridae and *Jynx*. A weak biventer with short fleshy bellies and a long tendon is seen particularly in the Upupidae, Phoeniculidae, Meropidae, Galbulidae and some Picidae. The anterior belly usually meets or lies close to its contralateral partner in the midline at the insertion, but right and left are separated by a wide gap in the Galbulidae, Meropidae (except *Nyctiornis*) and Picumninae.

M. spinalis cervicis and *M. splenius colli* (N.A.A.: *M. longus colli dorsalis*)

M. spinalis arises from the neural spines of vertebrae 14 to 18, and inserts by a series of slips on the anapophyses of 2, and of 6 to 13 (5 to 13 in *Malacoptila panamensis*). M. splenius colli has no independent insertion, but consists of a series of slips joining the slip of M. spinalis inserting on 2. There are from three to five of these slips, arising from the lateral surface of the neural spines of successive vertebrae, the most anterior in all cases being 4.

M. splenius capitis

In most species examined, this muscle arises from the neural spine of 2, and inserts on the posterior surface of the skull deep to M. biventer and M. complexus. In *Phoeniculus purpureus* and *Tockus erythrorhynchus* there was additional origin from the neural spine of 3. Right and left muscles generally lie close together in the midline, but a wide gap exists in *Melittophagus pusillus*. The muscle is relatively very large in the Galbulidae.

Cruciform structure of M. splenius capitis, as described by Burton (1971) is clearly evident in *Nonnula ruficapilla*, but barely discernible in most other species examined.

Mm. pygmaei (N.A.A.: *M. longus colli dorsalis, pars profunda*)

Mm. pygmaei are small, weak muscles, originating from the neural arches of vertebrae between 11 and 8, and inserting on the lateral edges of the transverse-oblique crests of vertebrae which are most commonly the second ones anterior to the vertebrae of origin. Asymmetrical distribution of Mm. pygmaei is frequent, and they are completely absent in most of the species examined here. They were found only in some species of Meropidae, Coraciidae, Leptosomatidae, Galbulidae and Bucconidae. Their occurrence in single specimens of various species in these families is as follows:

MEROPIDAE: *Melittophagus pusillus*. Left side, from 8 to 6 and 9 to 7; right side, from 8 to 6, 9 to 7, 10 to 8 and 11 to 9.

Nyctiornis amicta. Absent.

LEPTOSOMATIDAE: *Leptosomus discolor*. Left side, from 9 to 7 and from 10 to 8; right side, from 8 to 6.

CORACIIDAE: *Coracias benghalensis*. On both sides, from 8 to 6, 9 to 7 and 10 to 7.

Eurystomus orientalis. From 9 to 7 on the right; absent on the left.

GALBULIDAE: *Galbula ruficauda*. Left side, from 9 to 6; right side from 9 to 6 and from 8 to 6.

Galbalcyrhynchus leucotis. Present on the left side only, from 9 to 6 and from 8 to 6.

BUCCONIDAE: *Malacoptila panamensis*. From 8 to 6 and from 9 to 7 on both sides. Absent in *Notharcus macrorhynchus*, *Chelidoptera tenebrosa* and *Nonnula ruficapilla*.

Mm. ascendentes cervicis (N.A.A.: *M. cervicalis ascendens*)

Originating on the diapophyses of all cervical vertebrae except 1 to 5 these muscles each consist of two slips inserting on the anapophyses of the second and third vertebrae anterior to the origin. Thus, the most anterior muscle, originating on 6, inserts on 3 and 4. The series continues posterior to the neck as *Mm. ascendentes thoracicus*. No noteworthy variation was discovered among the species dissected.

M. longus colli ventralis

This large and complex muscle extends along most of the ventral side of the neck. The main part arises by a series of fleshy slips, starting in the thoracic region, from the sublateral processes, hypapophyses and the anterior region of the centra of successive vertebrae. Insertion is made by long tendons attaching on the cervical ribs; each vertebra sends a slip to join each of the tendons traversing it. In the anterior region of the neck, shorter slips arise from costal processes or sublateral processes, inserting tendinously on ribs or hypapophyses. Some of these anterior slips should perhaps be treated as *M. flexor colli profundus*; however, their siting and arrangement is so variable among the species studied that it seems impracticable to distinguish this as a separate muscle from *M. longus colli*.

Complete dissection of *M. longus colli* to enumerate the siting and arrangement of all slips throughout the study species, would be extremely time consuming. For the purposes of the present study, a more general examination was considered sufficient. The thoracic region was excluded, but particular attention was paid to the short anterior slips. The main features revealed are as follows: In all species, the most anterior insertion is on the hypapophysis of 2. Insertion on 3 is also on the hypapophysis, but on 4, insertion on the hypapophysis was found only in *Todus*, *Leptosomus*, and the representative species of Meropidae, Bucconidae, Galbulidae and Picidae; in the remainder, attachment on 4 is to the rib, or costal process. The slips attaching on 2, 3 and 4 are, in most species, short ones, arising typically from the sublateral process of 6, though the slip to 2 arises from the costal process of 5 in *Upupa*, and that to 3 from the sublateral process of 7 in *Phoeniculus*. The main part of the muscle, (consisting of long tendons and their associated fleshy slips) has its most anterior attachment typically on the rib of 5. In the Bucconidae and Galbulidae, long slips attach only as far forward as 6, but extend to 3 in *Upupa* and *Todus*, and to 2 in *Alcedo*, *Indicator*, *Jynx* and *Trachyphonus*. In *Momotus*, long slips attach on 2 and 4, but not on 3, while in the Picidae (other than *Jynx*), the entire muscle consists of long and very strongly tendinous slips attaching forward to 2.

M. flexor colli brevis (N.A.A.: *M. flexor colli lateralis*)

The bulk of this muscle originates from the lateral strut of 3 and the lateral processes of 4 and 5; origin on 5 is absent in *Alcedo atthis* and *Malacoptila panamensis*, while in *Campephilus* there is additional origin from the lateral strut of 6. The muscle also includes a smaller, medial portion, originating ventrally (typically on sublateral processes) and separated from the main body of the muscle by anterior slips of *M. longus colli*. (This portion may well represent a *M. flexor colli profundus*, merged with *M.f.c. brevis*; otherwise this muscle is

absent in the species studied). This medial portion appears to be absent in the species of Alcedinidae, Upupidae, Phoeniculidae, Bucerotidae, Bucconidae and Galbulidae dissected, and in some Picidae (*Sphyrapicus*, *Sasia*). It is present in the remainder, but varies considerably in development and in its relation to adjacent muscles (especially *M. longus colli*). In the species examined, it is best developed in *Trachyphonus darnaudii*, in which it actually originates posterior to the lateral portion, on the sublateral process of 6. In other species possessing it, the vertebrae of origin are the same as the lateral part except in *Momotus*, in which the very short medial portion originates from the postlateral process of 3.

Insertion is on the hypapophysis like process on the ventral side of the atlas (processus latus).

M. complexus

The sites of origin of this muscle vary considerably among the families investigated. No single species utilizes all the possible sites of origin, which are the anapophysis of 3; the transverse process and lateral strut of 4, and the diapophyses of 5, 6, 7, 8 and 9.

Insertion of *M. complexus* is on the dorsal edge of the occipitals, superficial to *M. biventer*. The muscle is best developed in the Alcedinidae, in which its origins have been checked in a wide range of species. Origin is from 5, 6 and 7 in the Cerylinae and Daceloninae, and from 8 as well in the Alcedininae; attachment to 9 was found in a single specimen of *Alcedo atthis*. Origin of *M. complexus* posterior to 7 has not previously been reported in any bird.

M. complexus is poorly developed in the Picinae (notably *Campephilus*) and in *Indicator*.

M. rectus capitis superior (N.A.A.: *M. rectus capitis dorsalis*)

This muscle lies superficial and anterior to *M. flexor colli brevis*, which it much resembles; the two could well be considered as divisions of a single muscle. Origin is from the lateral surface of neural arch 1, from the anterior surface of anapophyses 2 and 3, and in some species from the lateral strut of 4. Insertion is on the posterior edge of the basitemporal plate.

M. rectus capitis lateralis

This muscle inserts on the lateral edge of the exoccipital usually immediately lateral to *M. complexus*. Origin is commonly from the hypapophyses of 2, 3 and 4, and in *Leptosomus* and *Upupa* from 5 as well. However, the number of sites of origin is reduced in many species; 3 and 4 only are occupied in the Cerylinae and *Coracias*, and 2 and 3 only in the Todidae, Meropidae, *Eurystomus* and *Jacamerops*. Except for *Jacamerops*, reduction is even more marked in the Galbulidae and Bucconidae, with origin only from 3 in the species available for dissection. The muscle shows a corresponding reduction in bulk in these two families, and in *Notharcus macrorhynchos* and *Galbalcyrrhynchus leucotis* it can fairly be described as vestigial.

M. rectus capitis ventralis

Origin is from the ventral surface of 1, the hypapophyses of 2, 3, 4 and 5, and commonly also the sublateral process of 6. The latter point of origin is lacking in the Todidae, Momotidae, Meropidae, Phoeniculidae, Bucerotidae, Capitonidae and Ramphastidae. Insertion is on the basitemporal plate, anterior to *M. rectus capitis superior*. Both this muscle and *M.r.c. lateralis* are notably bulky in the Picinae, the very deep hypapophyses providing an increased area for their origin.

Mm. intertransversarii and *Mm. inclusi*

The *Mm. intertransversarii* connect successive vertebrae, running in most cases between their lateral processes. In the middle of their range, they are of complex, multipinnate structure (see especially Zusi & Storer, 1969). *Mm. inclusi* are similarly situated, but lie deep to *Mm. intertransversarii*, and are mostly divided into dorsal and ventral parts (*Mm. inclusi superiores* and *inferiores*). They end anteriorly one or two vertebrae before the *Mm. intertransversarii*. The most anterior *M. intertransversarius* in Coraciiform and Piciform birds is usually that between 5 and 4; in many species, lateral fibres from 6 also reach vertebra 4. The anterior limit is vertebra 3 in the Capitonidae, Picidae and Coraciidae.

PART 3

Functions and evolution

Bill and skull

The functional significance of bill form in birds is sometimes obvious, but more often rather hard to understand, even when it is distinctive or unusual. Bill modifications in the Coraciiformes and Piciformes are discussed at family level in the Systematic review; problems examined in this section concern more fundamental aspects of jaw action and cranial morphology.

Ideally it should be possible to integrate information on osteology and arthrology with that on muscle action to produce a complete picture of jaw actions and the ways in which they are controlled. In practice, however, this would require a very full understanding of the forces developed by muscles and their sequence of action, and of the physical properties of joints and ligaments. So far, the only analyses of avian jaw action which approach this ideal standard are those made for the Mallard (*Anas platyrhynchos*) by Zweers (1974, 1977). Work of this type, involving *in vivo* experimentation and electro-myography was beyond the scope of the present investigation, but the discussion which follows will at least serve to point out problems which would repay more intensive study.

Overall form

Barnikol (1952), following earlier work by von Kripp (1935) distinguished two general types of avian skulls which he called 'streckschädel' (stretched skull) and 'knickschädel' (hooked skull)*. He defined them in terms of two main criteria. In the 'streckschädel' type, the foramen magnum is situated at the back of the skull, and the brain axis makes a relatively small angle with the bill axis; in the 'knickschädel', the foramen magnum is situated more ventrally, and the brain axis makes a larger angle with the bill axes. Barnikol's examples of the former include *Cygnus*, *Ixobrychus* and *Phalacrocorax*; to them might well have been added various other members of their orders, as well as most of the Gaviiformes, Podicipediformes and some Procellariiformes and Charadriiformes. They are predominantly relatively primitive types specialized for aquatic feeding. The 'knickschädel' is much more widespread; Barnikol selects *Strix*, *Opisthocomus* and *Scolopax* as examples. He proposed, essentially, that the 'streckschädel' was a relatively archaic skull form which had become exaggerated for functional reasons in certain types, particularly fish eaters. He suggested, furthermore, that positioning of M. adductor mandibulae was an important underlying factor; evolution of the extreme 'streckschädel' allows the external temporal region of the muscle to be sited vertically above its points of attachment on the lower jaw. In the examples he chose, increasingly vertical attachments of M. add.mand.ext. are correlated with an increasingly vertical orientation of the postorbital ligament, which is finally sited slanting backwards to the mandible in *Phalacrocorax*.

The Coraciiformes and Piciformes are more advanced birds than any of Barnikol's 'streckschädel' types and the majority have skulls conforming fairly well to 'knickschädel' morphology. Nevertheless, there are significant variations in the orientation of major skull components, and these deserve to be considered in more detail. Among this assemblage, the Alcedinidae stand out as the clearest example of modification towards 'streckschädel' form, with skulls stretched out along the bill axis, and the palatal apparatus lying almost in the same plane as the tomia of the closed bill. However, difficulties are encountered when Barnikol's criteria are applied. By comparison with, for example, a *Megalaima* barbet, *Ceryle* has M.add.mand.ext. and the postorbital ligament less vertically oriented, while the situation of the foramen magnum scarcely differs. The elongated form of the *Ceryle* skull

*In discussions throughout this paper I shall use these terms in their German form, to indicate their origin clearly, to avoid possible ambiguities inherent in their English translations, and because they are less clumsy.

is, instead more clearly manifested in the low orbit and cranium, and in the arrangement of the kinetic apparatus, with the quadrates sited far back, behind the orbit. In ventral view, the pterygoids of *Ceryle* enclose a considerably smaller angle posteriorly than either *Megalaima* or any other bird included in this study.

It seems significant that the only members of the Coraciiform/Piciform assemblage to clearly show 'streckschädel' features of skull morphology are the one family whose members include fish eaters. Moreover, these features are much more strongly marked in the more thoroughly piscivorous Cerylinae and Alcedininae than in the Daceloninae. The functions and biological roles of 'streckschädel' modifications deserve much more study, but in the present instance, the following suggestions can be made:

(a) The combination of low orbits with a palate and bill oriented in a straight line brings the line of vision close to the primary axis of orientation of the bill (see Bock 1964: 28). This is probably of value in minimizing parallax error in a situation which is already complicated by refraction between air and water, and which may require great speed and accuracy in countering evasive action by prey.

(b) The skull increases in width from front to back; hence, by siting the quadrates, and thus the mandible articulation as far back as possible, the gap between the posterior ends of the mandibular rami is maximized. This may be an adaptation to swallowing large whole fish, since the rami themselves seem to have only a limited capacity for outward bowing. The long flat palate may also be helpful in this regard, since fish are long food items with less capacity for bending than much of the large prey, e.g. insects, frogs, taken by other Coraciiformes.

(c) The gradual, even taper of jaws and skull which is achieved through these modifications may be of some value in streamlining, to permit efficient movement through water.

The posteriorly situated quadrates of *Megalaima* mentioned above, are a rather unusual feature among the Coraciiform/Piciform assemblage, though characteristic of many Capitonidae and the Ramphastidae as well as Kingfishers. As in the Alcedinidae, this may well be an adaptation for swallowing large food items, in this case fruits, by increasing the gap between the mandibular rami. The accompanying feature of palatines, pterygoids and jugals lying more or less in the same plane as the tomia of the closed bill is more widespread, though only in the Alcedinidae does this involve the 'streckschädel' feature of a reduced angle between the pterygoids. It is seen particularly among the Coraciiformes, other than the Upupidae, Phoeniculidae and Bucerotidae, and in the Galbuloidea. In the Todidae, Galbulidae and still more the Meropidae, this is combined with a high cranium and very ventrally situated foramen magnum to produce skulls with an extraordinary profile, the front of the skull sloping down sharply to a low and rather flattened upper jaw base. This shape, and the position of the foramen magnum, is perhaps related to perching posture, in which the bill is normally tilted up at a considerable angle as the bird scans the sky for prey.

Viewed dorsally, considerable variation is seen in the extent to which the skull narrows from posterior to anterior. Narrowing in front of the orbits must be connected largely with the extent of forward vision. The most pronounced narrowing by far is seen in the Phoeniculidae, and is probably connected with feeding by gaping. Lorenz (1949) pointed out that passerine 'gapers' in the families Sturnidae and Icteridae look forward between the mandibles as they part them when feeding, and Beecher (1953a) showed that their ectethmoids are notched to increase their capacity for forward vision. It is puzzling that the Upupidae do not also have the skull narrowed in front of the orbits, since they feed in a similar manner, but on the ground. Perhaps the substrates in which they gape impose forces necessitating a more broadly based upper jaw.

The skull is also quite markedly narrowed in front of the orbits in the Indicatoridae, *Jynx* and many woodpeckers, again probably enabling them to look forward at prey or a substrate at close range. Moderate narrowing from posterior to anterior is seen in the Meropidae and Galbulidae, but in this case probably reflects more the distinct broadening of the posterior cranium in these families, a feature believed to be related to neck muscle action (q.v.). Most

other families examined have skulls which are relatively very broad anterior to the orbits, and this is in most cases undoubtedly related to the need for a large gape. In the case of the Alcedinidae this creates a problem, since as explained earlier, one function of their 'streckschädel' skulls seems to be to bring the line of vision as close as possible to the primary axis of orientation of the bill; the advantage of this adaptation would seem somewhat offset by the resulting reduction of forward vision. A partial compensation may be provided by the emarginated shape of the lacrimal.

Kinesis

The mechanics and functional significance of cranial kinesis in birds have been discussed at length by Bock (1964), who distinguishes two principal mechanisms. In *uncoupled kinesis*, the movements of the jaws are entirely independent; in *coupled kinesis*, depression of the lower jaw cannot take place without simultaneous raising of the upper. The principal structure on which coupled kinesis depends is the postorbital ligament, which is present in the majority of birds. An alternative way of achieving coupling is by means of an interlocking device at the quadrate/mandible hinge. This arrangement is uncommon, occurring sporadically amongst several unrelated groups of birds; these are listed by Bock (1964), and to this list must now be added *Bucorvus* and *Megalaima* (see p. 29–30).

Even where a postorbital ligament is present, uncoupled kinesis is possible when the ligament is unloaded (slack), a condition which occurs when M. protractor is contracting ahead of M. depressor. The mechanisms involved, and the variety of possibilities between strict coupling and total independence, are discussed by Zusi (1967), while Zweers (1974) provides detailed analysis of a closely coupled system in the Mallard. Some independent jaw action is even possible in forms with articulation lock coupling, such as *Bucorvus* and *Megalaima*, through spreading of the lower jaw rami. A critical point concerns the extent of retraction possible for the upper jaw in birds with coupled kinesis. Bock suggested that retraction past the normal closed position was impossible for birds possessing a functional postorbital ligament, but Zusi (1967) musters observational evidence to the contrary. Certainly at least some Coraciiformes and Piciformes are capable of this feat (see below). Presumably there is some relation between the extent of development of a postorbital ligament or articulation lock, and the extent and frequency of independent jaw action, but the relation is not a simple one, as indicated by the distribution of these features in families considered here. However, the possible biological roles of these mechanisms among Coraciiform and Piciform birds will be briefly reviewed as far as possible.

(a) COUPLED KINESIS. A closely coupled system appears particularly suitable where rapid jaw action is needed (Bock, 1964), and would seem particularly important for those species, mainly Coraciiform, which capture agile or aerial prey. The required acceleration must be achieved with minimum sacrifice of power, since the prey may need to be gripped strongly once captured—unless the initial snap of the jaws has sufficed to kill it, as must often be the case with small insects. Kinetic coupling may also be of special importance where forceful protraction of the upper jaw is required, in species which forage by 'gaping', i.e., inserting the jaws into the substrate and then opening them. Coupling in this situation enables the force of M. depressor mandibulae to be added to that of M. protractor (see discussions by Zusi, 1959, 1967; Manger Cats-Kuenen, 1961; Bock, 1964); this is of greatest importance in the Upupidae, Phoeniculidae and some Bucerotidae. *Bucorvus*, which possesses a well developed articulation-lock device obtains most of its food on the surface, but probably requires closely coupled jaw action for swift prey seizure. The significance of the weak articulation lock in *Megalaima* spp. is more puzzling, especially as they may have a significant need for independent jaw action in some circumstances (see below).

An aspect of coupled kinesis which has not received enough attention is the role of the musculature in guidance. This emerges very clearly from the work of Zweers (1974) on the Mallard, *Anas platyrhynchos*. The very strongly coupled kinetic system of this bird depends for its effectiveness on the action of the internal adductors in guiding the movements of quad-

rate, pterygoids and palatines. Exactly how the guiding and power roles of the jaw musculature would be fulfilled among the varied members of the assemblage studied here can scarcely be surmised at present. An understanding of this point would require much more precise information of their jaw movements than is at present available—a level of study possible only under controlled conditions in the laboratory.

(b) **UNCOUPLED KINESIS.** The independent jaw action made possible by uncoupled kinesis is important where skilful manipulation of food is at a premium, since upper and lower jaws are thus enabled to vary the angle and position in which they meet one another. A particularly valuable faculty in some birds is that of depressing the upper jaw past the normal closed position, with the lower jaw itself still partly depressed. The jaws can then be brought parallel, or even opposed with their tips closer together than the basal region. In bird photographs, evidence of retraction past the normal closed position is occasionally seen, when the tip of the lower jaw appears to extend beyond that of the upper, despite clearly undamaged bill tips.

Uncoupled kinesis is likely to be most needed when dealing with slippery or awkwardly shaped prey, or when several objects need to be gripped along the length of the bill. Thus, the weak development of the postorbital ligament in the Alcedininae and Cerylinae may be related to the need for skilful manipulation when dealing with fish. Retraction past the closed position is of limited extent in kingfishers, due to an effective retraction stop (see below), but apparently does occur; in a photograph of *Alcedo atthis* by Massny (1977) the lower jaw tip extends appreciably further forward than the upper. Among the Piciformes, similar problems may arise in dealing with large numbers of prey. Photographs of *Jynx* with a mass of ants held in the bill (Koffán, 1960) demonstrate independent jaw action excellently. The photograph shows the upper jaw tip retracted far behind the lower in a most convincing way. Note that the diagram of *Sphyrapicus* with the lower jaw projecting while closed in Spring (1965) must be of the bird with a damaged bill which the author refers to on p. 486; the position shown could not be attained by any normal jaw action. Barbets holding several fruits at once in the bill seem to face a similar problem (photograph in Thomson, 1964), but although most lack a postorbital ligament, they are not able to retract past the closed position, as further retraction is halted by a bony stop (see below). It is puzzling, though, that some Capitonidae have evolved a degree of articulation coupling, which has the same effect as a postorbital ligament, and for that matter, that the Ramphastidae have not.

Safety devices

During the processes of feeding and nest excavation, the skull is subjected to a variety of forces which have a profound influence on its morphology. Under the general heading of safety devices are included various osteological or arthrological features which serve to confine jaw and palate movements within safe limits, or otherwise to withstand potentially hazardous forces. Constraints, on movement are basically of two kinds; 'stops' are devices which limit the range of normal movement, especially that of kinesis, while guides and braces control direction and prevent abnormal movement caused by interaction with prey or objects in the environment. Stops are to be regarded as the final, ultimate limit on movement; in practice, the muscles and ligaments involved will normally arrest a movement before these extremes are reached. A review of kinetic stops, principally in waterfowl, is given by Fisher (1955).

As will be seen below, special modifications are present in woodpeckers to sustain forces incurred during excavation for food. It is interesting to note in passing that many other members of the Coraciiformes and Piciformes excavate wood or other hard substrates to create nest sites, yet lack special adaptations for doing so; even the frail skulls of the Todidae can cope with burrowing (Kepler, 1977). Presumably this is because nest excavation can be spread over a long enough time to allow even rather feeble excavating actions to suffice. Thus, the requirements of feeding remain the overriding force determining the architecture of skull and jaws.

Protraction stops

A potential stop on protraction in nearly all species is provided by the orbital process of the quadrate; when this touches the wall of the orbit, all forward movement of the palate must inevitably cease. How significant this is in practice is hard to judge. Some birds, such as typical Larids (Zusi, 1962), *Corvus* (Fisher, 1955) and some hornbills (present study) have a swelling on the orbital wall which would make early contact with the orbital process. In other birds, (notably the Alcedinidae in the present study), the position of the orbital process, far from the orbital wall, would render it quite useless as a stop. In between are a large number of birds in which the orbital process could possibly act in this way, but which lack special modifications. It is quite certain, however, that the orbital process cannot act as a stop in species which have *M. protractor quadrati* (q.v.) attached along its full length.

In this connection it is interesting to compare the Upupidae and Phoeniculidae with the Picidae (except *Jynx*). All three families have *M. protractor* greatly enlarged, and would seem to run an appreciable risk of dangerous over-protraction in the course of foraging. In the Upupidae and Phoeniculidae, the orbital process is free; it could well serve as a protraction stop, particularly in *Rhinopomastus*. These two families show no other obvious limitation on protraction, and it is possible that during the relatively slow action of 'gaping' there is little danger of sudden uncontrolled increases in this force.

By contrast, in the Picidae, *M. protractor quadrati* has attachment along the full length of the orbital process, and although it lies close to the orbital wall, it hardly seems possible for the two to touch, and thus stop protraction. Nevertheless, woodpeckers are at considerable risk. Hammering is assumed (Spring, 1965) normally to generate retraction forces on the bill, opposed by *M. protractor*, but a slight error, or unexpected irregularity in the wood might well add suddenly to protraction, instead of counteracting it. To safeguard against such eventualities, woodpeckers have an alternative stop mechanism in the form of a fronto-nasal hinge in which the frontal bulges out to overlap the upper jaw. This is not equally developed in all woodpeckers; Burt (1930) has demonstrated in a range of species that increasing development of this feature is correlated with increased size of *M. protractor*, decreased kinesis and greater dependence on hammering as a foraging method. Zusi (1962) has proposed a rather similar stop mechanism in *Rhynchops*, and the form of the fronto-nasal hinge suggests the same principle in various Strigidae and a few Falconidae. [The greatly developed casque of many Bucerotidae provides an alternative stop mechanism in the region of the fronto-nasal hinge, though this may not be its primary function; see Manger Cats-Kuenen, 1961].

Retraction stops

The fundamental stop on retraction occurs when upper and lower jaws meet; in addition, for most birds studied here, contact between the nasal bar and the dorsal anterior rim of the orbit (formed by lacrimal, ectethmoid or frontal) provides a further stop. This latter stop is discussed at length by Cracraft (1968), who points out that no locking mechanism exists which would eliminate muscular effort in retraction—a function of stops which had been proposed by Fisher (1955). In any case it is doubtful if such a device would provide any significant advantage, for reasons discussed elsewhere (Burton, 1978). The lacrimal-ectethmoid complex provides the firmest stop when a large ectethmoid forms or supports the stop. This condition is best realized here in the Upupidae, Phoeniculidae, Bucerotidae and Piciformes (other than Galbulidae and Bucconidae). The lacrimal forms the stop in the remainder except for the Momotidae which lack it, and rely on the frontal; even where it is much enlarged, as in the Alcedinidae and Coraciidae, it probably always produces a more resilient stop than the ectethmoid. In the Picidae, an additional stop is provided for many species by the very long anterior process of the opisthotic, which meets and articulates with the quadrate.

Cracraft questions why retraction stops are necessary at all, since the lower jaw would appear sufficient. He suggests that external forces encountered during feeding may produce unusual movements which require this safeguard. Among the families considered here, large

ectethmoids and firm retraction stops occur mainly in birds which excavate for their food (gapers and hammerers) and in fruit eaters; the latter may perhaps incur hazardous external forces during the wrenching movements sometimes needed to detach fruits from trees. Another situation in which retraction stops may be needed, not considered by Cracraft, would occur in uncoupled kinesis if the upper jaw is retracted past the normal closed position while the mandible remains partly depressed. In the Alcedinidae, this apparently occurs to a moderate extent, and the stop, formed by a large lacrimal, is indeed effective in bringing further retraction to a halt. It is interesting to note, though, that in a specimen of *Ceryle alcyon* with missing lacrimals, retraction much more extensive than could conceivably occur in life was possible without damage. Still more surprising, in *Jynx*, which regularly uses extensive retraction past the closed position, there is apparently no functional stop other than the limit imposed by the structure of the articulation of the quadrate and cranium. The fronto-nasal hinge here is simply flexible enough to sustain extensive retraction. Experiments with a freshly dead bird indicate a figure of approx. 20°–25° for the maximum retraction obtainable by muscle action, but by manipulation this could be extended to 55° without damage. Barbets and toucans mostly lack a postorbital ligament, and presumably have uncoupled kinesis, at least where there is no articulation coupling. Despite this, they apparently lack the capacity for retraction past the closed position, with retraction halting totally when the posterior medial surface of the ventral bar contacts the frontal, supported by a substantial ectethmoid.

Support of the jugal bar and palatines

Cracraft (1968) has described various modifications of the lacrimal-ectethmoid complex which appear to have the function of bracing the jugal bar against dorsally, and in some cases medially directed forces. He quotes Bock's (1960a) suggestion that the brace may prevent disruption of the jugal when food is being crushed, but notes 'of interest, however, is the fact that many species, which are close relatives of birds with a brace, lack the brace, but yet probably would derive advantage from possessing one'. This problem still remains unresolved, and this review only serves to re-emphasize it. Most Coraciiformes and Piciformes possess some sort of jugal brace, with the exception of the Momotidae, Capitonidae and, perhaps, Ramphastidae. In the latter family, the ventro-lateral corner of the ectethmoid is produced into a process which makes contact with the jugal bar where it broadens to join the maxillo-palatine—a position which scarcely seems to require bracing. Nor does this process seem to act as a retraction stop, for when skulls are manipulated, retraction is halted by the frontals before the maxillo-palatine makes effective contact with it. The slip of *M. pterygoideus* attached on the maxillo-palatine passes under the ectethmoid just medial to this process, but would be well flattened during strong retraction. The Capitonidae and Ramphastidae eat a large proportion of fruit, and apparently swallow much of it whole; possibly for these birds, the danger of disruption when crushing food is fairly small. The case of the Momotidae is much more puzzling, as much of their animal food surely requires fairly powerful crushing. Perhaps there is some positive selective advantage for losing the brace in this case, but it is difficult to see what this might be.

Bracing of the palatines by a wide ectethmoid is seen in a number of bird families feeding on aerial insects, e.g. Caprimulgidae, Apodidae, Hirundinidae. Cracraft suggests that it may serve to protect the palatines against impacts with moving prey. The Coraciiformes and Piciformes, although including various aerial insect feeding groups, show few clear examples of such a brace. The two principal families which feed in this way, the Meropidae and Galbulidae, catch their prey with the tip of a long bill, and forces on their palatines are unlikely to be abnormal. The Meropidae totally lack any indication of such a brace, while in the Galbulidae, *Galbula* has a wide ectethmoid lying near the palatine (though part of *M. pterygoideus dorsalis* intervenes between the two) but this is much reduced in *Galbalcyrrhynchus*. A possible ectethmoid brace exists, however, in *Indicator* and *Jynx*, though its function is unclear; perhaps it is connected in the latter with the large mouthfuls of insect prey which are collected to feed nestlings. In the Coraciidae, the anterior ventral

edge of the inflated lacrimal lies close to the palatine. In *Coracias* and the Brachypteraciinae, it is so far forward that it probably adds little to the support already available from the fused maxillo-palatines (see below). In *Eurystomus*, it lies somewhat further back, and may be of some value to this specialized aerial feeding genus, with its strongly widened palatines. *Chelidoptera* feeds in a similar way, but its ectethmoids are situated too far above the palatines to have any value as a brace.

Desmognathy

Much attention was given during the nineteenth century to the variations of palatal structure first described in detail by Huxley (1867). Attempts to interpret these at the time followed mainly phylogenetic reasoning, and surprisingly little attention has been paid to them since, despite the greater concern given to functional anatomy by more recent workers. Among the Coraciiformes and Piciformes the presence or absence of the desmognathous condition (in which the maxillo-palatines are fused in the midline) is a feature of considerable interest. It would appear that this condition is derived from a schizognathous or aegithognathous one rather than the reverse; various intermediate stages can be seen in the Capitonidae.

This condition is found throughout the Coraciiformes, but within the Piciformes it is seen only in the Galbuloidea, the Ramphastidae, and, weakly developed, in some Capitonidae. The Ramphastidae, like the Bucerotidae, have the anterior part of the palatines fused as well, producing the condition which Beddard (1898) termed 'doubly desmognathous'. This is presumably in some way a consequence of the evolution of massive bills in these two families, though whether through mechanical necessity or for ontogenetic reasons is uncertain.

The desmognathous forms include a large proportion of birds which feed on active, and often large animal prey, and it is possible that desmognathy provides some support against stresses incurred through killing and consuming such prey. Significant forces would be those acting across the bill axis; those acting along it are more a feature of birds which excavate for food, and resistance to them would scarcely be improved by midline fusion of the maxillo-palatines. Those acting across the bill include upward forces, produced by gripping or crushing prey, and lateral ones, either directly across or twisting (i.e. with a dorsal or longitudinal component). Simple upward forces would meet some resistance from well developed maxillo-palatines, but these need not necessarily be joined; the crucial feature of fusion seems most relevant where lateral forces are involved. An important factor here may be the technique of beating prey against the perch, used by many species to kill or immobilize their victims. This is commonly performed sideways, and though the prey is the primary target, the bill often makes contact with the perch as well. The forces involved are necessarily large, since feeble blows would fail in their purpose. It is perhaps significant that passerines lack midline fusion of the maxillo-palatines, their expanded vomers supporting them only against moderate dorsally directed forces. Although some passerines, such as crows and shrikes, regularly take large and vigorous prey, their methods of subduing it do not include the highly developed beating behaviour of the Coraciiformes and Galbuloidea.

Desmognathy has also some relevance to the evolution of an *M. pterygoideus dorsalis* with attachment on the maxillo-palatine, as seen in several Coraciiform and Piciform groups. Such an attachment requires at least a strong maxillo-palatine; since unilateral action could impose severe stress on the maxillo-palatine, desmognathy would seem to be almost essential as well. In fact, the majority of species in which *M. pterygoideus* is attached on the maxillo-palatine are desmognathous. Exceptions occur only among the Capitonidae, in which slight muscle attachment on the maxillo-palatine is present in some species which are scarcely or not all desmognathous; any increase in such attachment, however, might be expected to be closely accompanied by increased desmognathism. This may have been a key factor in the evolution of the Ramphastidae from barbet ancestors (see Systematic Review, pp. 433–434).

Pterygo-palatine articulation

The Indicatoridae and the Picidae (including *Jynx*) differ from all other families studied here in the form of the pterygo-palatine articulation, with a long pterygoid foot overlapping the

palatine dorsally and medially. This arrangement would seem less prone to disarticulation than the short articulation of other families, but it is far from clear why it has only arisen in these two groups. The change may have involved transfer of the epipterygoid from the palatine (with which it normally fuses) to the pterygoid, but no nestlings were available young enough to compare its ontogeny between these two families and others.

Lower jaw

The movements of the lower jaw are generally simpler than those of the upper, except insofar as the two are correlated by kinetic coupling. An exception to this is seen in birds which possess the capacity to widen the gap between the mandibular rami by the action of *M. pterygoideus ventralis medialis*; the pull of this muscle on the internal process of the mandible rotates it on the quadrate articulation, bowing the rami outwards. Though this mechanism has been described from various unrelated taxa, such as the Procellariiformes and Charadriiformes (Yudin, 1961), Columbiformes (Burton, 1974*b*), Caprimulgiformes (Bühler, 1970, 1980) and probably *Pelecanus* (Burton, 1977*b*), it appears to be absent, or scarcely developed in most Coraciiformes and Piciformes. Flexible zones within the mandibular rami are obviously a prerequisite, but are virtually lacking in the majority of species examined. A small degree of flexibility which would permit moderate bowing seemed to be present in skulls of *Alcedo*, *Leptosomus* and *Jynx*, and with fresh material might be demonstrated in a few more. Nevertheless, this faculty seems to be of little significance in the feeding methods of the Coraciiform-Piciform assemblage. This is somewhat surprising in view of the many members of this assemblage which swallow large prey whole. Presumably flexible rami would be incompatible with other mechanical demands, such as those of prey beating. It should also be noted that Coraciiform and Piciform birds do not feed their young by regurgitation, a process which involves mandible bowing in some groups of birds.

For the majority of birds, there is relatively little danger of excessive depression of the lower jaw—an event only likely to be brought about by unusual environmental forces, such as those encountered by *Rynchops nigra* (Zusi, 1962). Consequently, there is no system of bony stops, the main limitation on movement being the post orbital ligament, acting in conjunction with the upper jaw apparatus. However, the lower jaw is exposed to other hazardous forces, for which various support mechanisms exist, as follows:

(a) *The internal and external jugomandibular ligaments.* The internal ligament resists backward disarticulation; the external resists downward and perhaps forwardly directed forces. Both are present throughout the families studied except the Picidae. Their lack of the external jugomandibular ligament is presumably directly related to the development of the opisthotic ligament which partly takes over its function.

(b) *The occipito-mandibular ligament.* Universally present (though very weak in *Jynx*), and very strongly developed in the Upupidae, Phoeniculidae and Bucerotidae. In at least the first two of this group of families, the large size of the ligament is likely to be related to feeding by gaping and probing. The occipito-mandibular ligament resists forward disarticulation of the mandible, and forces tending to cause this are most likely to reach significant levels when the bill is being extracted from some substrate (see Burton, 1974*a* for discussion of this situation as it affects probing shorebirds).

(c) *The quadrate condyles.* The primary role of the condyles is, of course, in articulation of the mandible in normal movement. However, the form of the medial condyle in some families studied here suggests a possible additional function in resisting disarticulation. This is most clearly seen in the Bucconidae, in which the medial condyle projects ventrally well beyond both the other condyles and the pterygoid articulation. It is flattened in the same plane as the pterygoid, and oriented to project slightly forwards and outwards; the tip is swollen and rounded. Less extreme versions are seen in the Galbulidae, Coraciidae and Leptosomatidae and to some extent even in the Momotidae and Meropidae.

Experimentation with prepared skulls quickly shows that this deep medial condyle would be ineffective in resisting anteriorly or posteriorly directed forces, but firmly resists a force

acting medially. Forces acting across the jaw in this way may well arise during prey beating, a technique regularly employed by these families, or when swallowing large prey. Kingfishers lack a deepened medial condyle however, despite the fact that they beat fish vigorously, and consume quite large ones whole.

It should be emphasized that a medial condyle of this form must inevitably have other functions as well. It must play an important part in coupled kinesis, although it is unable to bring about coupling in itself, like the specialized medial condyle of *Bucorvus* and some barbets. Its shape is highly efficient for spreading the mandibular rami during jaw closure, though admittedly this also happens perfectly well in birds with an unspecialized medial condyle. Its depth, in the *Bucconidae* especially, brings the centre of rotation of the lower jaw unusually far below the cranium; the significance of this is unknown. It certainly merits much further study, for it may be an important feature in the evolution of the *Galbuloidea* and *Coraciiformes* (see *Systematic Review*, p. 430).

(d) *The medial brace*. This feature was first described in *Rynchops nigra* by Shufeldt (1890) and subsequently in a wide range of birds by Bock (1960a). Its functions in *Rynchops* were further studied by Zusi (1962).

As Bock points out, all structural features of the brace suggest that it serves to prevent disarticulation of the mandible when the bill is opened. He further proposes that it compensates for inadequate protection by the quadrate condyles when the jaw is widely opened. The distribution of the brace among the families examined here supports these proposals. The brace occurs only in families which regularly feed on large or active prey, and often need to open the jaws widely; it is absent in groups which are primarily fruit eaters and in those which probe or excavate for insect prey. Three families appear to form an exception; these are the *Leptosomatidae*, *Galbulidae* and *Bucconidae*, all of which lack a medial brace. However, these are also families possessing a very deep medial quadrate condyle. This provides a high degree of protection for the articulation, even with jaws open (see above), and also has the effect of holding the lower jaw so far from the basitemporal region of the cranium that secondary articulation is impossible.

On the basis of this reasoning, a deep medial condyle or a medial brace might seem to be alternative derived mechanisms fulfilling the same function. They are not necessarily mutually exclusive, however. The *Coraciidae*, for example, seem clearly to have a common origin with the *Leptosomatidae*, and still possess a fairly deep medial condyle (rather reduced in *Eurystomus*), but have a medial brace as well. Perhaps during the evolution of the *Coraciidae*, the medial condyle has been reduced due to some other factor(s) to the point at which a basitemporal articulation—and thence, a medial brace—could develop. The medial brace thus needs to be treated with some caution if used as a taxonomic character.

Jaw muscles

M. adductor mandibulae externus

M. add. mand. ext. raises the mandible; it also retracts the mandible against the quadrate, rocking it backwards about its articulation with the cranium, and thus aiding retraction of the palate and depression of the upper jaw. (*M.a.m.e. caud.*, arising on the quadrate, is unable to affect the upper jaw in this way). It is generally the most complex of the jaw muscles, and its structure varies greatly among the *Coraciiformes* and *Piciformes*. Fortunately, sufficient information is now available from other orders to give at least an outline picture of its evolutionary history. This wider perspective is essential, for the structural diversity of the muscle cannot be adequately interpreted in purely functional terms.

Among species studied here, the most complex *M. add. mand. ext.* is seen among the *Phoeniculidae*. In this family, the muscle includes several well defined components which are absent from the great majority of birds of other orders so far studied. An important exception is provided by the *Anatidae*; many members of this family possess a complex *M.*

add. mand. ext. which is remarkably similar in its components and arrangement to that of *Phoeniculus* and *Rhinopomastus*. An approach to this condition is also shown by some Charadriiformes, e.g. *Chionis* (Burton, 1974a). In the comparative discussion which follows, reference should be made to Table I for clarification of the terminology used for this muscle by previous workers; a fuller account of synonymy for M. add. mand. ext. is given by Starck & Barnikol (1954).

The complex condition of M. add. mand. ext. seen in the Phoeniculidae and Anatidae is characterized by two main features:

1. The presence of a postorbital lobe, i.e. a section originating directly from the postorbital process, dorsal to M.a.m.e. rost. temp. This is represented in some families (e.g. Alcedinidae, Upupidae) by a single slip, but in its fully developed form (e.g. Phoeniculidae, Anatidae), there are two parts. The dorsal part arises fleshily from the postorbital process, and is attached to the mandible via an aponeurosis, while the more ventral and medial one arises by an aponeurosis from the postorbital process, and its fibres fan out across the lateral surface of the mandible.

2. A relatively narrow insertion of M.a.m.e. vent. The fan shaped sheet of fibres arising from Ap. 2 which constitutes this division of the muscle in most birds is replaced by similar sheets also inserting on the lateral surface of the mandible, but arising from either the postorbital lobe (ventral part), or from an expanded M.a.m.e. caudalis, or even from M. adductor posterior. This arrangement, but without a postorbital lobe, is also seen in Picidae (other than *Jynx*).

Regarding the first of these features, although the evolutionary history of the postorbital lobe has been little discussed by previous workers, its presence in the Anatidae at least is well documented. It was noted by Lakjer (1926) in *Oedemia* (= *Melanitta*) *nigra*, and included in his terminology for M. adductor mandibulae externus superficialis, which is approximately equivalent to M.a.m.e. rostralis as understood here. The same terminology was followed by Goodman and Fisher (1962) in their study of waterfowl. A complication found in the Anatidae (but not the Phoeniculidae) arises from the coalescence of the post-orbital and zygomatic processes. This has merged M.a.m.e. vent. with M.a.m.e. rost. Starck and Barnikol (1954, Fig. 11) regard M.a.m.e. vent. (= Ap. 2 portion) in *Anas platyrhynchos* as the lower half of a bipinnate muscle whose dorsal part is M.a.m.e. rost. temp. (= Ap. 1 portion, ex. temp.). Lakjer (1926) and Goodman and Fisher (1962) treat the whole unit as M.a.m.e. superf., 1a portion ('levator anguli oris'). If Starck and Barnikol are correct, which I believe to be the case, then M. add. mand. ext. medialis (MII) of Lakjer and of Starck and Barnikol is not equivalent to M.a.m.e. vent.—as, on terminological grounds it should be—but, roughly, to M.a.m.e. rost. med.

Turning to the second feature noted above, particular interest centres on the contributions of M.a.m.e. caudalis and M. adductor posterior to the more ventral and posterior sheet of muscle on the lateral surface of the mandible. In the Phoeniculidae, (as in the Picidae, discussed later) this is provided entirely by fibres from M.a.m.e. caudalis. Interestingly, this is also the case in *Chionis* (Charadrii), leading Yudin (1965, fig. 71) to label it incorrectly as M. add. mand. medialis (= M.a.m.e. vent.). (See Burton, 1974: 122).

Among the superficially similar Anatidae, however, the situation is more complicated. Here, M.a.m.e. caudalis itself is not widely expanded, but is closely associated, or even fused with an extensive lateral insertion of M. add. post. This has led to some confusion. Lakjer (1926) figured *Oedemia* (= *Melanitta*) *nigra*, which happens to be a species in which M.a.m.e. caudalis is somewhat reduced, and completely overlaid anteriorly by M. add. post.; his figures 121 and 122 depict this correctly, a point I have checked by dissection. Goodman and Fisher (1962) who follow Lakjer's terminology, also label the fibres on the ventral lateral surface of the mandible as M. add. post. in other waterfowl, though in the two of their figured species which I have dissected (*Spatula clypeata*, *Mergus merganser*) the posterior edge of

this group of fibres is contributed by M.a.m.e. caud. (But note that Goodman and Fisher's 'a' and 'b' parts of M. add. post. do represent a real division of this muscle in *M. merganser*). Starck and Barnikol (1954) go to the opposite extreme by labelling the equivalent region in *Anas platyrhynchos* as 'Ap. 3 post.' (= M.a.m.e. caud.). In this species (and *S. clypeata*) M. add. post. and M.a.m.e. caud. are thoroughly fused, but most of the lateral fibres come from M. add. post., as in other ducks. In a goose, however, (*Anser anser*, fig. 29), Starck and Barnikol label the lateral ventral fibre sheet as M. add. post. Clearly there is scope for much further investigation of the relative development of these two muscles, and not only in waterfowl.

Although the similarity between M. add. mand. ext. in the Phoeniculidae and Anatidae does not extend to all points of detailed structure, there are still enough features in common to require explanation, the more so since clear echoes of the same condition are seen in some Charadriiformes. These three groups can scarcely be considered as close relatives, and it is difficult to envisage convergence as a factor in such totally different birds. More probably, the complex state of M. add. mand. ext. in the three groups should be regarded as a primitive feature, and similarly any traces of it which remain in other families, e.g. the postorbital slip in kingfishers, or the narrow M.a.m.e. vent. and extensive M.a.m.e. caud. in the Picidae. Probably future studies will reveal similar conditions in other groups, and perhaps shed further light on the evolution of components of M. add. mand. ext.

As a corollary of this view, the simpler structure seen in most birds is a derived one; this is characterized by a narrowly inserting M.a.m.e. rost. lacking any postorbital lobe, and M.a.m.e. vent. which alone forms the sheet of fibres inserting on the lateral surface of the mandible, and a short M.a.m.e. caud., situated deep and partly concealed by M.a.m.e. vent. This general derived condition is widespread, and has clearly arisen more than once, and probably many times. It can therefore scarcely be regarded as a useful taxonomic character in itself, any more than can the presumed primitive state. Nevertheless, detailed comparison reveals differences between groups which are consistent enough to be significant, such as those between the Coraciiformes and Piciformes. Such consistent differences may indicate that the simplified condition was derived independently in the two groups.

It may be noted that the Phoeniculidae still retain the primitive condition, and thus the Upupidae and Bucerotidae which seem closely related to them (see p. 426–429) probably represent two more independent lines in which a simplified condition has been attained among the Coraciiform/Piciform assemblage.

It is interesting to observe that here again, as in many other respects, the Galbulidae and Bucconidae resemble the Coraciiformes rather than the Piciformes. The position within the Picidae is also somewhat unclear; the derived condition is only fully developed in *Jynx*, which resembles barbets, toucans and honeyguides in its wide, flattened M.a.m.e. rost. lat., and in the form of M.a.m.e. vent. The implications of this are discussed further in the systematic review (p. 434).

So far, there has been little consideration of functional aspects. In the foregoing discussion, an underlying assumption has been that the components of M. add. mand. ext. function simply to contribute to the forces of adduction and retraction, rather than possessing distinctive additional functions of their own. This is, no doubt, an oversimplification, but one that probably comes fairly close to the truth, leaving unaffected the general evolutionary picture which has thus far been depicted. Any distinct local functions of components of M. add. mand. ext. would probably concern stresses on the mandibular ramus; thus, for example, the balance between the forces of M. add. mand. ext. on the lateral surface of the mandible and M. pseud. prof. on the medial surface must in some degree influence the structure of both muscles. However, adduction and retraction remain overriding factors, the contribution of components varying with their situation. The more dorsal parts of the muscle have a greater moment arm, and consequently provide more force in adduction; they also act over the greatest distance, and generally show fairly simple fibre arrangements. In passing, it may be noted that the most dorsal component of all (in the absence of a postorbital lobe), M.a.m.e. rost. temp., normally has strongly bipinnate structure. This is the inevitable result of the

way in which its fibres are attached, around the edges of the temporal fossa. A parallel fibred structure would waste much of the potential surface for origin. Ventral parts, particularly M.a.m.e. caud. have a shorter moment arm, and also act over a shorter distance; in consequence, strongly multipinnate fibre arrangements are characteristic of this section of the muscle (see Gans & Bock, 1965).

Although components within a complex M. add. mand. ext. like that of *Phoeniculus* may have only limited significance individually, the overall result is a bulky and presumably strong muscle, with extensive aponeurotic surfaces for fibre attachment. Birds which have attained a simpler structure in this muscle have lost some potential sites for origin or insertion of fibres, and may, when required, create new ones by branching of existing aponeuroses. This is well illustrated within the passerines (e.g. Bock, 1960*b*) or among waders (Burton, 1974*a*). In such cases of secondary structural complexity, a region of the muscle which is often elaborated is M.a.m.e. rost. med.—as, for example, the 'Ap.D. slip' of the Scolopacinae described by Burton, 1974*a*. Within the Coraciiformes and Piciformes, M.a.m.e. rost. med. is relatively poorly developed; perhaps because M.a.m.e. rost. temp. has remained well developed in many members of the two orders.

The exact extent of M.a.m.e. rost.temp. does, nevertheless, vary a good deal among the birds studied here, and, as in many groups, there appears to be a distinct correlation with body size. (And also with reduction of the lateral portion of M. pseudotemporalis superficialis). A very limited temporal origin is characteristic of small species, and is often associated with overall simplicity of muscle structure, and reduction in pinnate fibre arrangements. This is, no doubt, simply one of the many consequences of the relation between body size (weight varying as the cube of linear dimensions) and strength of components (proportional to cross sectional area, and hence their square). It is tempting to speculate, however, that fluctuations in size within the line ancestral to a species may have influenced its present structure. To take M. add. mand. ext. as an example, structural simplification may in many cases have arisen within small species; components which disappeared in such species could have thus been lost forever, even if their descendants subsequently evolved larger body size.

M. pseudotemporalis superficialis

Among the families considered here, this muscle ranges from a bulky structure of complex architecture to a slip which is vestigial or even absent. A crucial point in understanding this variation appears to be the relative development of lateral and medial regions of the muscle. A highly developed lateral lobe can with confidence be regarded as a primitive feature of the muscle, being exhibited by several unrelated non-passerine groups. In some of these—e.g. among the Laridae—it extends substantially onto the temporal surface of the skull, deep and somewhat dorsal to M.a.m.e.rost.temp. Reduction of this lateral portion appears to be an evolutionary trend common to many avian groups, and generally strongly correlated with reduction of M.a.m.e.rost.temp. In the groups surveyed, a lateral portion is best developed in some families of Coraciiformes, and within this order there is little development of a medial region, even where the lateral origin is much reduced. Where marked reduction has occurred, the whole muscle has become dorsal and superficial in character, lying mainly lateral to the Vth cranial nerve. The Galbulidae and Bucconidae resemble the Coraciiformes in this respect, but the condition is even more strongly marked, the muscle being vestigial in many species, and absent in some. In typical Piciformes, by contrast, there is generally a well marked medial extension of the origin, as though in compensation for loss of the lateral; the whole muscle is generally more medial and deep in position, lying more or less medial to the Vth cranial nerve.

The factors underlying these differing trends are hard to discern in our present state of knowledge. It is by no means clear why reduction of one part of M. pseudotemporalis superficialis should be compensated by enlargement of another, if, indeed, this is what has actually happened in the Piciformes. A trend towards reduction and loss of the muscle as seen in the Coraciiformes appears more reasonable; it would seem relatively simple for M. add. mand. ext. and M. pseudotemporalis profundus to take over the task of M. pseudotemporalis

superficialis in providing adduction force with a component medial to the mandibular ramus. Some answer may eventually emerge from a deeper understanding of cranial architecture.

M. pseudotemporalis profundus and *M. adductor posterior*

Like *M. pterygoideus*, *M. pseudotemporalis profundus* acts both to raise the lower jaw and (through its action on the orbital process of the quadrate) to depress the upper jaw. Relative development of the muscle is hard to assess; its apparent size in dorsal view is certainly a most unreliable guide. In the majority of birds, its excursion is a long one, a fact reflected in its largely parallel-fibred structure; the main exception here is shown by *Tockus erythrorhynchus* in which the muscle is small, with its insertion relatively close to the centre of rotation of the mandible. Otherwise, the most significant variation is the total absence of the muscle in many Alcedinidae. This is certainly related to the form of the skull in this family, in which palatines and pterygoids lie almost in the same plane, and the quadrate has swung backwards (by comparison with other birds), so that the orbital process lies very close to the mandible. Only a small *M. pseudotemporalis profundus* is therefore possible in any case, and loss of the muscle is not surprising. Even more extreme versions of this skull form are seen in a number of other fish eating groups (Barnikol, 1952), and loss of *M. pseudotemporalis profundus* has also occurred in some of these, e.g. *Sula*, *Phalacrocorax* (Hofer, 1950). A similar quadrate shift, accompanied by loss of *M. pseudotemporalis profundus* has also taken place (though for different morphological reasons) in the Psittaciformes (Hofer, 1950; Burton, 1974c). It is interesting to note that the muscle is present in some Cerylinae, but absent in others; detailed observation and comparison of feeding actions in members of this subfamily might produce interesting results.

M. adductor posterior, by reason of its situation so close to the quadrato-mandibular joint and consequent short moment arm, can play little part in adduction, but has been suggested to act in providing support for the lower jaw on the quadrate (Zusi, 1962). It shows relatively little variation among species studied here. The lateral expansion seen in some barbets would somewhat increase its capacity for adduction; this may be a primitive feature (see discussion under *M. add. mand. ext.*).

M. pterygoideus

Because this muscle is attached at one end to the mandible, and at the other to the palatal complex, it acts both to raise the lower jaw and to retract the palate and thus depress the upper jaw. The siting and structure of components of the muscle may favour one or the other of these two main actions, and functional accounts of *M. pterygoideus* inevitably concentrate on these two aspects. Although an analysis in these terms goes part way to explaining the structural complexity of the muscle, it leaves a number of questions unanswered in the case of the Coraciiformes and Piciformes. Satisfactory answers will probably require a much more detailed understanding of jaw mechanics than we at present possess.

Particular interest centres on the division of *M. pterygoideus dorsalis* into lateral and medial portions, and on the modifications of each. Two families examined (Upupidae and Phoeniculidae) showed no division into two portions; nor does *Ramphastos toco* (Ramphastidae). All but one of the remaining families have the muscle divided by a groove into which *N. pterygoideus* passes, shortly after diverging from the mandibular ramus of the Vth cranial nerve. The exception is the Bucerotidae, in which a clear groove divides the muscle, but the nerve penetrates it an appreciable distance posterior to the groove. (If the raphe of the bipinnate *M. pter. dorsalis* in *Phoeniculus purpureus* is considered homologous with the dividing groove, then this genus shows a similar condition). A similar situation was found among the Charadrii studied by Burton (1974a). A reasonable explanation for such a dichotomy would be to regard the undivided condition as primitive, and the two positions of nerve relative to groove as alternative derived conditions; however, the possibility cannot be excluded that a divided condition may return to an undivided one. Even less clear is the functional relevance of the division.

Physical separation by a groove implies that these two parts of the muscle perform quite

distinct actions. M. pter. dors. lat. is oriented more nearly parallel to the long axis of the skull, and hence would act more effectively as a depressor of the upper jaw; at the same time, its more anterior placement on the mandible would improve its capacity for adduction. M. pter. dors. med. seems badly situated from both points of view; in the case of the passerine genus *Loxops*, Richards & Bock (1973) suggest that it functions mainly to rotate the pterygoid (to which it is largely attached) during kinesis. However, in many of the birds examined in this study, M. pter. dors. med. extends far onto the palatine, and may be so oriented as largely to overcome its disadvantageous position for palate retraction. In such cases, the muscle is functionally almost equivalent to a completely undivided M. pter. dorsalis. Groups showing this condition of M. pter. dors. med. may have M. pter. dors. lat. attached to the maxillo-palatine (see below) or much reduced, as in the Galbulidae. In some Galbulidae, M. pter. dors. lat. is approaching a vestigial condition, and interestingly, one of them (*Jacamerops aurea*) shows a partial division of M. pter. dors. med. in a similar situation to the groove which divides M. pter. dors. lat. from M. pter. dors. med. in the majority of birds. (Total loss of M. pter. dors. lat. would leave N. pterygoideus in the curious situation of entering the muscle via its anterior edge.) The evolutionary reasons for this development remain obscure, and do not seem to be correlated in any obvious way with changes in skull architecture. The Bucconidae generally resemble the Galbulidae in the narrowing and reduction of M. pter. dors. lat., yet one of them (*Chelidoptera tenebrosa*) surprisingly retains a M. pter. dorsalis divided by a groove in the normal position.

A feature of much interest revealed by this study is the attachment of M. pter. dors. lat. to the maxillo-palatine in several families. This feature has not been previously described in any bird, even in Starck's (1940) study of the Bucerotidae. Attachment to the maxillo-palatine was found in the Alcedinidae (excluding the Cerylinae), the Phoeniculidae, Bucerotidae, many Capitonidae and Ramphastidae. The significance of this modification is not immediately clear. The maxillo-palatine may simply act as a useful additional surface for muscle attachment, permitting the development of a bulkier M. pter. dors. lat. However, it should be noted that by attaching on the maxillo-palatine, M. pter. dors. lat. depresses the upper jaw directly, and not via the medium of the palatal complex. It is possible that such a fundamental innovation may have other advantages than simply to increase the force for adduction of the lower jaw and depression of the upper. Possibly a careful comparative study of jaw movements in related birds differing in this feature (similar sized members of the Daceloninae and Cerylinae would be highly suitable) might shed further light on this point.

It may be noted that the presence of a bipinnate M. pter. dors. lat. is not correlated with attachment on the maxillo-palatine, although both features occur together in most Alcedinidae and the Bucerotidae—and in *Phoeniculus purpureus*, in which the bipinnate structure of the entire M. pterygoideus dorsalis is functionally equivalent to that of M. pter. dors. lat. alone. Other groups in which bipinnate structure occurs are some Momotidae and Indicatoridae, and more moderately in the Picidae (except *Picumnus* and *Jynx*). The feature might be expected to relate to a need for powerful contraction over short distances, as when the extent of jaw opening is small, or in isometric contraction with the jaws held open. Small amplitude jaw movements are probably important in many kingfishers and woodpeckers, and maintenance of a position with jaws slightly parted may be essential during drumming or chiselling by woodpeckers (Spring, 1965; Bock, 1964, 1966). Prolonged isometric contraction would also seem to play a part in manipulation of large fruits by some hornbills, though toucans face similar problems and do not have a pinnate M. pter. dors. lat.

Finally, the retractor palatini slip of M. pter. vent. med. requires comment. Among the groups considered here, this feature occurs only in the Upupidae, Phoeniculidae and Bucerotidae. However, a similar modification is found also in many passerines (e.g. Fiedler, 1951; Bock, 1960) and some other orders (Burton, 1974c). The families showing the feature here differ from others in the sheer size of the retractor palatini slip, and in its extensive attachment on both palatine and pterygoid; it appears to comprise all of M. pter. dors. med. post. plus part of M. pter. vent. med., whereas in passerines, M. pter. dors. med. post. remains

(at least partly), in unmodified form (see Richards & Bock, 1973). (The presence in *Tockus erythrhorhynchus* of a raphe similar to Ap. N is a further point of difference.) The retractor palatini differs from all other parts of *M. pterygoideus* in that its action is purely to retract the palate and depress the upper jaw; it cannot adduct the mandible at all, nor can it bring about mandible howling as described by Yudin (1961), Zusi (1962) and Bühler (1970). Thus, it would be of great importance in any feeding action for which independent operating of the upper jaw was required. Small manipulative actions in long-billed birds are probably often of this type (Burton 1974a), and its presence in the Upupidae and Phoeniculidae may be related to such needs in these probing feeders. (But note that there is no retractor palatini in the many Scolopacidae which employ a combination of deep probing and skilful manipulation in feeding; their rhynchokinetic upper jaws are more than adequate to meet these needs.) The Bucerotidae obtain their food in a variety of other ways, but their retractor palatini may be a heritage from ancestral forms possibly rather similar to the Upupidae and Phoeniculidae.

M. protractor quadrati et pterygoidei

The action of this muscle is to pull the pterygoid forward and medially, and to rock the quadrate forward and upward about its articulation with the cranium. These movements are communicated to the upper jaw, causing it to be raised.

Noteworthy development of the muscle occurs in the Upupidae and Phoeniculidae; and in the Picidae. In the former two families, the condition of *M. protractor* is almost certainly related to their probing habits. These two families also have a large *M. depressor mandibulae* attached to a long retroarticular process. Both features are adaptations for 'gaping', i.e. opening the bill against the resistance of a substrate in order to excavate a wider hole in which to seek prey. Similar modifications are seen in some Charadrii, e.g. *Scolopax* (Marinelli, 1928; Burton, 1974a) and a variety of Passeriformes, e.g. the Icteridae (Beecher 1953a) and Callaeidae (Burton, 1974b). Among the Piciformes, enlargement of *M. protractor* is presumably connected with its function as a shock absorber during hammering as proposed by Beecher (1953b, 1962) and Spring (1965). It is of considerable interest to note that the muscle is not enlarged in *Jynx*—a point which will be discussed further in the systematic review later in this paper.

Some confusion has arisen concerning *M. protractor* in the Bucerotidae, apparently as the result of a misunderstanding. Hofer (1950), referring to Starck (1940) in a footnote on p. 438 says 'Dass ein *M. protr. pterygoidei* bei *Buceros* fehlt, ist auffällig und verlangt eine erneute Untersuchung anderen Bucerotiden.' However, Starck makes it quite clear that *Buceros* does possess a *M. protractor*, a fact which I have checked on a specimen of *B. rhinoceros*: Hofer's misinterpretation apparently arose from Starck's remarks on the muscle treated here as the retractor portion of *M. pterygoideus*. It is unfortunate, however, that no spirit specimen of *Rhinoplax vigil* was available. The extraordinary kinetics of this bird have been clarified by the very detailed osteological study of Manger Cats-Kuenen (1961), but it would be of great interest to examine its jaw musculature also, especially *M. protractor*.

Differentiation into two clear parts appears largely to be connected simply with the extent of development of the muscle as a whole. A more puzzling aspect is the extent of attachment to the orbital process. In most birds considered here, attachment on the quadrate was limited mainly to the body and mandibular process, but there seems to be no obvious common feature separating these from the species in which extensive attachment on the orbital process was found. It may be relevant to note that fibres attached on the postero-medial side of the orbital process are directly antagonistic to *M. pseud. prof.*, attached on its antero-lateral surface. Injury to the orbital process caused by *M. pseud. prof.* can occur (Burton, 1972), and possibly a better understanding of this point may be achieved by more detailed study of the action of these two muscles as a paired and antagonistic unit.

M. depressor mandibulae

M. depressor acts to depress the lower jaw; it probably also plays a part in elevating the

upper jaw, through its upward force component on the quadrate (Bock, 1964; Zusi, 1967; Bühler, 1980). The connection between enlargement of this muscle and the 'gaping' method of excavating food has been noted above under *M. protractor*. Among the Coraciiformes and Piciformes, such enlargement occurs only in the Upupidae and Phoeniculidae, with some indication of a retroarticular process also in the Bucerotidae. The fact that *M. depressor* is not markedly enlarged in the Picidae supports the view that the great development of *M. protractor* in this family is unconnected with gaping.

Tongue, hyoid, and hyoid musculature

Tongue and hyoid skeleton

The tongue is greatly reduced in the Alcedinidae and Upupidae, and very small also in the Phoeniculidae and Bucerotidae. In the Alcedinidae, this reduction is presumably related to the consumption of fish; several other groups of fish eating birds show similar tongue reduction, notably among the Pelicaniformes and Ciconiiformes. Clearly, a long tongue would be ineffective in manipulating such relatively large and slippery prey, but the small structure which is retained is fully functional, and presumably aids in swallowing. It may be noted in passing that although various kingfishers include insects, reptiles and other prey in their diets this is not accompanied by any enlargement of the tongue. On the other hand, groups such as the Coraciidae and some Bucconidae which consume relatively large prey, but not fish, have relatively large tongues.

In the Upupidae and Phoeniculidae, different factors have produced a similar result. These birds include many small insects in their diets, but these are obtained by probing in firm substrates, such as earth or wood. Their decurved bills are strongly reinforced, and for much of their length there is no lumen in which a tongue could be accommodated. Similar factors have led to tongue reduction in some shorebirds, e.g. *Numenius* (Burton, 1974a). The Bucerotidae in general have bills which could accommodate a longer tongue, so their short tongue condition is more difficult to explain; possibly their ancestry included a stage resembling the present day hoopoes. Sheer bill size is certainly no bar to tongue elongation, as the Ramphastidae demonstrate.

The distribution of brush tongues is more puzzling. Tongues with their tips or edges split into laciniae are found in three families of Coraciiformes, in a few Galbulidae and Capitonidae, and in the Ramphastidae. They do not relate in any simple or obvious way with food, as birds showing this feature have diets ranging from small insects through vertebrates to fruit. There is obviously much scope for further investigation of this feature, and not only within the orders considered here. The dense small papillae on the basal region of the reduced tongues of the Upupidae, Phoeniculidae and Bucerotidae probably serve to improve their friction grip.

Of all tongue modifications within the two orders, however, the most intriguing is certainly that exhibited by the Picidae. The enormously long 'tongue' in this family actually includes only a relatively tiny horny tongue and entoglossum; the greater part of its extended length consists of the elongated basihyal, and the approximated anterior ends of the ceratobranchials, sheathed in epidermal tissue derived from the buccal floor. The advantage of this arrangement is that a capacity for tongue movement and manipulation is retained even while probing deeply in an insect burrow; if the horny tongue alone were elongated as in many nectar feeders, such as the Trochilidae, its articulation with the basihyal would lie much too far back to allow useful movement within a confined space. An analogy to the tongue extension of the Picidae is seen in the bills of many Scolopacidae, which have the zone of kinetic bending in the upper jaw shifted far forward, so that fine movement is still possible at the bill tip, even while probing deeply (Burton, 1974a, Marinelli, 1928).

Although the tongue and hyoid of the Picidae seem at first sight so different in structure from those of their relatives, some indication of how they evolved can still be gained by

examining other families of typical Piciformes. Several structural characteristics suggest that among these families the tongue has assumed a role in which forceful protraction and manipulation are of greater importance than in the Coraciiformes, or, perhaps, many other orders. The relatively long, narrow basihyal is one of these, adding considerably to the effective length of the tongue. Such a tongue would be less effective when pushing large food items backwards, by retraction; for this purpose it is better for the basihyal to be short, yet wide enough to provide adequate anchorage for *M. stylohyoideus* and *M. thyrohyoideus*, as in the Coraciiformes. The entoglossum is generally more thoroughly ossified than in the Coraciiformes, also suggesting a more forceful role, and in a number of species shows a curious double structure, with anterior and posterior halves connected by a narrow region which is cartilaginous in some. Possibly this makes possible some degree of passive bending which may be useful in prey manipulation, making up in part for the absence of *M. ceratoglossus* anterior which confers a degree of independent tongue tip bending in many birds. The ultimate development of a very long basihyal and short tongue makes this unnecessary in the Picidae, which show at best only slight indications of the entoglossum shape of their relatives.

Hyoid musculature

M. mylohyoideus

Contraction of this muscle raises the floor of the mouth. The extent of its variation within the Coraciiformes and Piciformes remains unclear, and therefore cannot profitably be discussed at present.

M. ceratohyoideus

This muscle pulls the hyoid horns medially, opposing the lateral force component of *M. branchiomandibularis*. Its reduced condition in the Alcedinidae is perhaps not surprising considering the feeble development of *M. branchio-mandibularis* in some members of the family. However, the total loss of *M. ceratohyoideus* in the Indicatoridae is not accompanied by any reduction of *M. branchiomandibularis*. In the Picidae, which also lack it, medial movement of the horns is imposed during protraction as they slide forward within a cylinder of tissue derived from the buccal mucosa.

M. stylohyoideus

The main retractor of the tongue, and also capable of deflecting the tongue to one side, by unilateral contraction. *M. stylohyoideus* is essential if the tongue is to be used effectively for thrusting food backwards in the buccal cavity. An alternative means of propelling food backwards is by means of head jerking, and this is likely to be the most effective method where food items are relatively very large—e.g., fish, frogs or lizards, as consumed by several families of Coraciiformes. Diets of this type are associated with tongue reduction, and it is perhaps not surprising that there is also a tendency towards reduction of *M. stylohyoideus* in the Coraciiformes. Total loss has occurred in the Bucerotidae, which rely heavily on head jerking to propel food backwards, but its near loss in the Todidae is more unexpected.

M. stylohyoideus also appears to have been lost in the Coraciidae, Galbulidae and Bucconidae, but its place is taken by a slip which is apparently a part of *M. serpihyoideus*—though possibly a *M. stylohyoideus* whose insertion has completely shifted to the ventral surface of the hyoid skeleton. This unusual arrangement is certainly a derived character, and its presence in just these three families must inevitably provoke some phylogenetic speculation (see p. 149–150).

M. branchiomandibularis

This muscle is the protractor of the tongue, responsible for pulling it forward to manipulate food or even to capture it, as in woodpeckers. The enormous development of *M. branchio-mandibularis* in the Picidae is obviously essential to bring about the extensive protrusion of which their tongues are capable; similarly its virtual absence in some kingfishers is

connected with a vestigial condition of the tongue, which plays little part in food manipulation.

A more intriguing point concerns the surprising variability in its sites of origin, seen mainly among the Coraciiformes. Among birds of other orders and in several families studied here, *M. branchiomandibularis* originates simply from the medial surface of the mandible. Probably, therefore, this is the normal (= primitive) condition, and origin on the buccal mucosa or mandibular symphysis is a derived feature. If this view is correct, these unusual sites of origin probably arose through gradual anterior extension of the origin along the medial surface of the mandibular ramus. Thus, the Upupidae and Phoeniculidae would represent a transitional stage in a shift of origin to the mandibular symphysis. Origin on the ventral surface of the buccal mucosa is less easy to interpret. This condition usually occurs in combination with attachment on the mandibular ramus, and may simply be another way of gaining an increased area for origin; alternatively, it might have arisen by secondary reduction from attachment at the mandibular symphysis.

Before this interpretation can be adopted with confidence, however, it would be desirable to understand the relation of *M. branchiomandibularis* and *M. genioglossus* more fully. The latter muscle is absent in many of the birds studied here, as also in very many other birds. However, where present, its origin is from a ledge at the mandibular symphysis similar to that from which *M. branchiomandibularis* arises in several families. There is no correlation between the presence of *M. genioglossus* and any particular state of *M. branchiomandibularis*. Nevertheless, it is possible that the presence of an *M. genioglossus* was a necessary condition for the shift of *M. branchiomandibularis* origin to the mandibular symphysis, even if *M. genioglossus* itself has subsequently been lost. If so, forms showing spread of *M. branchiomandibularis* origin onto the mucosa only may have developed their extension of origin subsequent to loss of *M. genioglossus*. A further possibility which cannot be discounted is that a muscle resembling *M. genioglossus* could arise *de novo* from *M. branchiomandibularis*. A condition which could conceivably serve as a preliminary state for such an event is seen in the Todidae; the medial slip of this muscle would only need to lose its attachment to the epibranchiale to become indistinguishable from *M. genioglossus*. Much more study of these and other birds will be required to clarify the relation between these two muscles, and such study should certainly include close examination of their ontogeny.

Variations in siting of the origin of *M. branchiomandibularis* also prompt speculation as to their functional significance. Forward extensions of origin obviously result in a longer muscle, and therefore, potentially a greater capacity for tongue protrusion. However, this is of little value without enlargement of the tongue and hyoid skeleton, and in practice birds which do show modifications for extensive tongue movements (such as the Picidae, or nectar feeders, notably the Trochilidae) have achieved these almost entirely by lengthening the hyoid horns, and thus the insertion of *M. branchiomandibularis*. Alternatively, the use of new sites of origin might have arisen simply to enlarge the muscle as a whole, and hence its potential force. This is also an unsatisfactory explanation, since the space available for insertion on the epibranchiale sets a limit on the bulk of the muscle; moreover, many of the birds possessing an anteriorly sited origin have small tongues for which forceful action seems unnecessary. This problem must remain unresolved at present, but further study might well consider the possible significance of the change of plane which has resulted from change in origin. The horizontally flattened *M. branchiomandibularis* seen in birds with an origin on the mandibular symphysis or buccal mucosa may have important effects on the floor of the buccal cavity itself, additional to its action in tongue protraction.

M. genioglossus

An effect on the buccal cavity is a possible action of this muscle; Bock and Shear (ms., mentioned by Richards & Bock, 1973) suggest that the pair of *Mm. genioglossi* act as a set of guides along which the tongue slips as it is protruded. Whatever its functions, any clarification of them which results from future work may also provide some explanation of modifications of *Mm. branchiomandibularis*, as discussed above. Since so many birds lack *M.*

genioglossus, it may be that even in some which possess it, the muscle no longer has any biological role, and merely awaits the genetic changes necessary to bring about its total loss.

M. ceratoglossus

This muscle depresses the entoglossum, and with it the tongue, relative to the basihyal. It is a short-fibred, unipinnate muscle, capable of exerting substantial force; this is particularly so in those birds which have enlarged the area for fibre origin by extending onto the basihyal. This feature occurs in the Indicatoridae, Capitonidae and Ramphastidae, and in the two latter at least may be related to a need for powerful manipulation of fruits and other large food items.

M. ceratoglossus anterior and M. hypoglossus medialis

These two small muscles, where present, act via the median aponeurosis to depress the tip of the horny tongue relative to its bony or cartilaginous base; *M. hypoglossus medialis* can also act (like *M. ceratoglossus*, s.str.) to depress the tongue relative to the basihyal. Their distribution in birds generally is patchy and difficult to explain. Among those reviewed here, they occur mainly in insect eaters, notably the Meropidae and Galbulidae; they may thus be of some value in the manipulation of insect prey, particularly the potentially hazardous venomous Hymenoptera which both consume.

However, the biological roles of these muscles cannot be reliably discerned until their evolutionary history has been clarified. Both muscles appear to have a scattered distribution amongst a variety of birds of several orders, suggesting that their presence is a primitive feature. Against this, they are relatively simple structures, probably derived from neighbouring muscles, and performing a distinct action not duplicated by other muscles. Consequently, they might have appeared independently in unrelated groups, or might even reappear secondarily after an initial loss. This question could very likely be solved by checking for these muscles in a much wider range of birds than so far studied; a more comprehensive picture of their distribution might reveal some significant pattern. It must be remarked that such a search would need to re-examine many groups whose tongue musculature has already been studied, as they have certainly been overlooked in some accounts, possibly due in part to nomenclatural confusion.

M. hypoglossus obliquus

Contraction of this muscle depresses the posterior end of the entoglossum. If right and left muscles contract together, the tip of the tongue will be raised, but unilateral contraction will also deflect the tip of the tongue to the ipsilateral side. Unilateral action is presumably possible only in muscles of Type 2; where right and left have merged into a continuous loop (Type 1), elevation of the tongue tip is the sole function of the muscle. Only the Todidae showed the Type 1 condition in the groups studied here; probably their small invertebrate prey require little reorientation prior to swallowing, and lateral tongue movements may thus be of less importance.

The modified elongated form of Type 2 seen in the Upupidae, Phoeniculidae and typical Piciformes is of special interest. Because of the considerable length of *M. hypoglossus obliquus* in these birds, a large part of the muscle is oriented at only a very small angle to the basihyal. Where insertion is made via an aponeurosis as in the Indicatoridae and Picidae, individual fibres may be oriented more steeply to the basihyal, but the line of action of the whole muscle is nevertheless very nearly parallel to the basihyal. Thus, although the muscle as a whole may be much larger (and therefore capable of exerting more force) than in the normal condition, its range of action may be more limited. This is simply because a fibre (or aponeurosis) attaching on the paraglossale cannot elevate the tongue past the point at which the two are in line; only fibres situated well anteriorly are able to raise the tongue tip appreciably above the axis of the basihyal. The modified form of Type 2 will thus do little more than to bring the tongue into line with the basihyal, and even its range of lateral action will be more limited. It will still, of course, be essential for returning the tongue from

a depressed position (as brought about by *M. ceratoglossus*), but this provides no explanation for the evolution of the elongated form of the muscle.

The importance of this modification probably lies in its effect when contracting synergically with *M. ceratoglossus*. The two muscles will then provide a strong backwardly directed force on the tongue both above and below its pivot on the basihyal tip. In this state, tongue and basihyal form a single rigid unit, capable of forceful probing actions. Such an arrangement was doubtless a crucial preadaptive condition permitting the evolution of the highly adapted probing tongue of woodpeckers. This differs from those of other Picidae principally in its relatively much longer basihyal, producing an *M. hypoglossus obliquus* so long that it appears exactly like a dorsal version of *M. ceratoglossus*—hence the term '*M. ceratoglossus superior*' used by Leiber (1907*a* & *b*). The factor triggering this transformation must simply have been the abandonment of virtually all forms of diet other than those obtained by tongue probing, and consequently the abandonment of the more versatile tongue which other typical Piciformes still retain. It is probably significant that the nearest approach to the *M. hypoglossus obliquus* of the Picidae is shown by the Indicatoridae, which have a narrow diet including many insect grubs, for which forceful tongue probing may be an important feeding technique.

M. tracheohyoideus and *M. tracheolateralis*

Much interest attaches to the pattern of distribution of the two alternative sites of origin of *M. tracheohyoideus*, which acts as a retractor of the tongue and trachea. The simplest explanation for the distribution found is to suppose that origin on either the midline or laterally on the clavicle are both derived conditions, the primitive situation (represented here only by the Bucerotidae) being that in which both sites are utilized. If this view is correct, a shift from one site to the other seems unlikely and this dichotomy is therefore of considerable phylogenetic significance (pp. 423 & 430). The generally small amount of variation in *M. tracheolateralis* seems, by contrast, to be of no great interest.

M. thyreohyoideus

This muscle retracts the tongue relative to the larynx. Within the Coraciiformes and Piciformes it shows little variation requiring comment, save to remark that its great length in the Picidae is a simple consequence of the elongation of the basihyal in that family.

The neck

Cervical vertebrae

Many of the structural variations noted are probably of only minor significance. Thus, the reduction or loss of fused ribs in the Bucerotidae and Picidae, though a derived feature, must surely have occurred independently in the two families. Similarly, the bony struts connecting costal or transverse processes with the lateral crest may well be a primitive feature, but their gradual reduction must have proceeded independently in many families.

Fusion of the first and second vertebrae in the Bucerotidae is of some interest. This feature, which seems to be virtually unique among birds, presumably provides more firm support for the relatively heavy head and bill, but there are many other groups of birds which face similar problems but lack this modification. Beddard (1898) found the same feature in a specimen of *Chunga*, probably the one in the British Museum (Natural History) registered 1870-10-5-1, which does indeed show such fusion. However, another specimen of the same species (*C. burmeisteri*) has the atlas and axis quite separate, as do specimens of the closely related *Cariama cristata*.

Beddard (1898) discussed the significance of a subvertebral canal (as seen in the Picidae) at some length. Outside the Coraciiform/Piciform assemblage it also occurs in the Podicipediformes, Pelecaniformes and Ciconiiformes. Although the canal encloses the carotids, it seems unlikely that it is necessary for their protection. More probably, its value lies simply in the increased area which it makes available for attachment of the fleshy slips of the highly

developed *M. longus colli ventralis*. It is interesting to note that there is some development of a subvertebral bridge in *Jynx* and even in *Indicator*, perhaps denoting an early stage in specialization for excavation.

Cervical musculature

Excellent discussions of the actions of the neck muscles and some factors which have influenced their evolution in *Rynchops nigra* are given by Zusi (1962). Comparative accounts for the Charadrii and the Callaeidae (Burton, 1974a & b) provide further information on the functional significance of various structural modifications. However, many problems concerning their evolution remain to be answered. An issue of particular importance has been raised by a recent study of Charadriiform phylogeny (Strauch, 1978). In this numerical investigation, Strauch utilizes data on neck muscle attachments obtained from my earlier study (Burton, 1974a). In processing this information, he makes the assumption that evolutionary changes in points of origin or insertion involve only loss of attachments, not gains. This may well be a reasonable working hypothesis. It is certainly true that among birds as a whole, large numbers of neck muscle attachments (and large numbers of vertebrae) are found mainly in groups considered to be of relatively ancient origin (e.g. Podicipediformes, Anseriformes), while they are markedly reduced in more recent groups such as the Passeriformes, or the families studied here. Moreover, the genetic and developmental processes by which cervical muscles might evolve additional origins would seem to be different from those required for most other muscles; extension of origin for a cervical muscle requires that a gap be crossed between one vertebrae and the next. Jaw or tongue muscles, by contrast, could evolve a larger origin by a series of small expansions over a continuous bony surface, e.g., the temporal surface of the skull for *M.add.mand.ext.rost.temp.* Nevertheless, the possibility that cervical muscles may sometimes evolve additional sites of origin should not be entirely discounted.

Among the birds studied here, a case in point concerns the origins of *M. complexus* among the Alcedinidae. No other birds, of any order previously investigated possess such posteriorly sited slips of origin; vertebra 6 is the posterior limit in most groups, and many species have an *M. complexus* originating no further back than 5, or even 4. Previous to this investigation, the only reported exceptions were in *Spheniscus demersus* (Boas, 1929) and *Tryngites subruficollis* (Burton, 1974a), both of which have attachment on 7. Kingfishers, however, have attachment at least as far back as 7, and on 8 or even 9 in the Alcedininae.

A scattered distribution among unrelated groups like this is often an indication of a primitive feature. Paradoxically, however, the situation within the Alcedinidae alone seems to suggest just the opposite. The extra sites of origin appear of obvious adaptive value in enabling *M. complexus* to cope with the heavy head and bill which are a specialized feature of the family. Moreover, the greatest posterior extension is seen in the Alcedininae, which are highly specialized fishers, and not in the more primitive and generalized Daceloninae. On such evidence, the simple explanation would be that the extra origins are also a derived feature, evolved *de novo* for functional reasons. If, on the other hand, they are indeed a primitive feature, it may be supposed that they were more widely distributed among birds at the time the Alcedinidae evolved; thus, their retention in this one family would be due to their specialized role, while the majority of birds, lacking the same needs, have lost them.

Similar problems arise with several other neck muscles whose sites of origin vary in an apparently functionally significant way (see *M. splenius capitis*, below, and Burton, 1974a), and a full answer will require much more knowledge of the genetic and developmental mechanisms controlling them. Such further research might initially be best concentrated on *Gallus gallus*, or some other domestic bird whose genetics and embryology are already well known.

M. biventer cervicis

This muscle acts both to tilt the head upwards on the atlas, and to straighten sections I and III of the neck and flex section II upwards. Unilateral contraction would tend to turn the

head to one side, but this effect would be very limited except in groups which have the insertions of right and left muscles separated by a wide gap.

The very marked enlargement of *M. biventer* in the Alcedinidae is undoubtedly connected with the need to maintain posture of the relatively heavy head, which may often be further burdened with a bulky item of prey. Working synergistically with the ventral neck muscles, the muscle may also have an important role in stabilizing head attitude while diving. The role of the transverse aponeurosis between right and left muscles is obscure. It would act to limit unilateral action, or to prevent spreading of the anterior bellies, but why these functions should be needed is unknown. Its distribution within the family is equally enigmatic, since it occurs throughout a group of specialized fishers (the Cerylinae), but also in a scattering of relatively primitive forest dwelling forms among the Daceloninae.

M. biventer cervicis is also noticeably enlarged in *Jynx* and *Indicator*, a fact which may be connected with their habit of excavating for insects and their larvae. However, specialized excavators such as the Upupidae, Phoeniculidae and Picidae generally show reduction of *M. biventer*. In the Picidae at least, this is probably because much of the task of delivering blows has been transferred to the pelvic musculature, the neck functioning chiefly as a rigid support for the head—a point discussed further under *M. longus colli ventralis*.

M. biventer is weak also in the Galbulidae and Meropidae, but left and right muscles are separated by a considerable gap at their insertion on the relatively wide cranium. They are thus situated well out from the pivot of atlas and occipital condyle, an arrangement which may help to modify or control lateral head movements of these highly manoeuvrable aerial feeders (see Burton, 1977a).

M. spinalis cervicis and *M. splenius colli*

These muscles together act to straighten sections I and III, flex section II upwards, and raise I and II relative to II and III. Unilateral action will also bring about lateral bending. Although there is some variation in site of origin, particularly of *M. splenius colli*, this does not appear to fall into any significant pattern.

M. splenius capitis

This muscle acts to tilt the head upwards, and if contracted unilaterally, to turn it to one side as well. Where origin from 3 is present, the fibres involved should exert a greater torque, since they are farther from the pivot of the cranium, and are therefore likely to be important for actions requiring the exertion of large forces.

Among those with attachment only on 2, the muscle is most notably enlarged in the Galbulidae—a feature related, perhaps, to their adroit aerial manoeuvres during the pursuit of prey. Enlargement in this family is made possible by the very extensive occipital area available for insertion.

The utilization of 3 as an additional site of origin in *Phoeniculus* and *Tockus* also makes possible a more bulky muscle. Combined with the greater torque of the posterior fibres, this origin may be important for the excavation techniques of the former, and control of the relatively large head in the latter. In the Charadrii (Burton, 1974a), there is a rough correlation between presence of an origin on 3, and the use of probing or other vigorous feeding techniques. Nevertheless, there are many exceptions to this relationship, as also among Coraciiform and Piciform birds; for instance, *Upupa* and many kingfishers might equally seem to have a need for this modification. As in the case of *M. complexus*, Strauch (1978) regards *M. splenius capitis* origin on 3 as a primitive feature, and this is probably correct. Thus, its distribution could be explained by assuming that retention would be more likely in lines for which this extensive origin acquired a special biological role relatively early; while those lines which lost origin on 3 before such a role appeared, have been unable to evolve it again. However, as in the case of *M. complexus*, the possibility of extra origins arising *de novo* cannot be discounted in the present state of our knowledge.

Mm. pygmaei

These muscles act to flex section I of the neck upwards. Their small size, patchy distribution

and frequent asymmetry combine to suggest that they are of little adaptive value among the birds studied here, and are being gradually eliminated. Obviously, their presence is to be regarded as a primitive feature, and hence of no taxonomic significance. It is interesting, however, to note in passing that of the five families possessing them, four are considered to share a common origin in the phylogeny proposed in the conclusion to this paper.

Mm. ascendentes cervicis

The actions of this series of muscles are similar to those of *M. spinalis cervicis*, with additional capacity for lateral bending. They appear to lack significant variation in structure among the species studied here.

M. longus colli ventralis

This large and complex muscle plays a major role in downwardly directed movements of the neck, flexing sections I and III, and straightening section II. The short anterior slips have an independent action on section I. A general pattern seems to emerge of greater emphasis on the short slips among birds whose feeding actions involve relatively small forces, and greater development of long slips among birds with vigorous feeding techniques, such as hoopoes, kingfishers and woodpeckers. However, the relation is far from clear cut, and much more detailed study of this muscle is obviously needed. The most extreme modification of *M. longus colli* occurs in the Picidae, with short slips eliminated, and very broad and strong tendons for attachment of the long slips. This is, in fact, the only really notable specialization of neck musculature seen in this family, despite repeated loose statements in the literature referring to the highly developed neck muscles of woodpeckers. Its role in the Picidae is evidently to maintain the neck as rigidly as possible in a downward flexed position during hammering, the actual force of the blows being imparted to a large extent by movements of the entire body. Doubtless *M. longus colli* works synergistically with dorsal neck muscles in maintaining this rigidity, but it is the muscle primarily responsible for resisting the upward bending forces resulting from interaction with the tree trunk.

M. flexor colli brevis

Bending section I upwards is the principal action of this muscle; unilateral contraction will also produce lateral bending. The small variations in structure observed are probably of little adaptive significance.

M. flexor colli profundus

The action of this small muscle supplements those of the anterior slips of *M. longus colli ventralis*, and it is probably subject to similar selective forces. However, as explained under *M. longus colli*, the factors underlying the balance between long and short slips will not be adequately understood until much further study has been carried out.

M. complexus

The principal action of this muscle is to tilt the head upwards. Once upward tilting of the head has reached its limit, further contraction will straighten section I. Unilateral action will turn the head and bend section I sideways. A further action is possible if the muscle has origin posterior to section I; it is then capable of raising section I relative to section II. Among the Coraciiformes and Piciformes, only the Alcedinidae possess this ability, with slips of origin as far back as 8, or in one individual *A. atthis*, 9. The muscle is also strikingly bulky in this family.

Kingfishers have relatively very large heads, and their prey are often heavy. Presumably the large *M. complexus* provides a major part of the force necessary to maintain head posture. Its origins posterior to section I may indicate that in many actions, head and section I maintain a constant configuration, and are moved as a unit on section II. The extra length of *M. complexus* in kingfishers may also be advantageous in holding head and neck firmly in line when diving. An *M. complexus* ending at 5 or 6 would act at a less favourable angle for maintenance of head posture in the extended position, though the difference would be much less marked in the perched position, with head horizontal. The relatively short necks of kingfishers exaggerate this effect.

As discussed earlier, it would be of great interest to know whether the extensive origin of *M. complexus* in kingfishers is a primitive or a derived feature. If genuinely primitive, then this may have been a key factor enabling the family to evolve their fishing adaptations. An allied question, discussed in the systematic review, concerns whether the fishing behaviour itself is primitive in the group or not.

Woodpeckers have a comparatively small *M. complexus*. This is perhaps not surprising, since in this family, the head is kept flexed downward for much of the time whilst foraging, and the main emphasis is on the ventral cervical musculature (see under *M. longus colli*).

M. rectus capitis superior

Contraction of this muscle flexes the head and section I downwards. It is generally shorter in the Coraciiformes and Piciformes than in the Charadrii studied by Burton (1974a), but little significant variation was encountered in the species studied.

M. rectus capitis lateralis

Upward tilting of the head is the primary action of this muscle; unilateral contraction will contribute to turning the head and bending Section I sideways. Its actions serve only to reinforce those of *M. complexus* and *M. splenius capitis*, and the muscle shows reduction in many species studied here. Extreme reduction of the muscle, as in the Galbuloidea, has not previously been reported in other birds, and is presumably related in some way to the large size of *M. splenius capitis* in this family.

M. rectus capitis ventralis

This is the bulkiest and most important of the muscles acting to tilt the head downwards. It can also bend section I downwards, and where attachment to 6 is present, may act to swing section I downwards relative to section II. Unilateral contraction will contribute to sideways bending. The bulkiness of the muscle in the Picidae is its most noteworthy modification here, a feature clearly related to the need for sustained downward flexion of the head while foraging and excavating in woodpeckers.

Mm. intertransversarii and Mm. inclusi

Though producing some dorsoventral movement, the major importance of these muscles is probably in producing sideways bending of the neck, or in resisting lateral forces. They also contribute to the support of articulations between vertebrae. The level of detail studied here was not sufficient to permit useful comparisons of function between species.

PART 4

Systematic review

Introduction

This final section summarizes characteristic features of the feeding apparatus for each family, and discusses their taxonomic and functional implications. At the same time, it enables problems requiring further study to be pointed out. Discussions of inter-family relationships should ideally, perhaps, be organized to follow the groupings recognized by Peters (1945, 1948). However, the findings of the present study fall into a pattern radically different from Peters' classification, and such a treatment would make a clear exposition difficult. Instead, the fifteen families studied have been arranged into four groups on the basis of feeding apparatus structure. These are:

- (a) Typical Coraciiformes: Alcedinidae, Todidae, Momotidae, Meropidae, Coraciidae (including Brachypteraciinae) and Leptosomatidae.
- (b) Hoopoes and Hornbills: Upupidae, Phoeniculidae and Bucerotidae.
- (c) Galbuloidea: Galbulidae and Bucconidae.
- (d) Typical Piciformes: Capitonidae, Indicatoridae, Ramphastidae and Picidae.

It may be noted that on the basis of evidence produced by Feduccia (1977), group a. might well have been subdivided. The four group arrangement is retained, however, but Feduccia's proposals are discussed at some length in the concluding sections of this review.

No attempt is made to discuss theoretical concepts in phylogeny reconstruction and classification, but the phylogenetic reasoning followed pays due regard to the points raised by Cracraft (1972).

Typical Coraciiformes

Skull and jaws are highly variable in form and proportions, but always have a complete maxillo-palatine bridge, the quadrate usually with a prominent medial condyle. A post-orbital ligament is present in all but a few Alcedinidae, and the lower jaw has a secondary articulation (medial brace) in all families except the Leptosomatidae. M.a.m.e.rost.lat. is limited in extent, and sometimes vestigial or absent, while the expanded anterior part of M.a.m.e.vent. lies well forward, exposing M.a.m.e.caud. to lateral view. M.pseud.superf. generally has an extensive lateral origin, but its medial region is reduced; NV passes under the muscle towards its medial side, quite near the dorsal surface, with the ramus pterygoidei and ramus mandibularis usually running close together for some distance. The origin of M.pseud.prof. on the orbital process of the quadrate is usually a broad one. M.pter.dors.lat. is rather narrow in many, but sometimes bipinnate in structure, and with attachment to the maxillo-palatine in the Alcedinidae. The tongue varies much in development, but the entoglossum is always largely cartilaginous, and the basihyal fairly short. M.stylohyoideus is reduced in the Todidae and absent in the Coraciidae, but replaced in the latter by a slip from M.serpihyoideus. M.branchiomandibularis takes much or all of its origin from the ventral surface of the buccal mucosa in most species. M.genioglossus is present in the Momotidae, Meropidae and Coraciidae. M.tracheohyoideus originates on the clavicle. Mm.pygmaei are present in some Meropidae, the Coraciidae and Leptosomatidae. Dorsal components of the neck musculature, concerned with raising the head, are particularly well developed in the Alcedinidae.

ALCEDINIDAE

The feeding apparatus shows numerous distinctive features, many of which appear to be related to fish eating. This suggests that fish have for a long time been an important element of diet in the history of this group, even though some species have turned to an entirely terrestrial way of life. Basic feeding strategy in most species is to wait for prey from a lookout point, captures are fairly infrequent, but prey are relatively large. A similar strategy is used by some other Coraciiformes, e.g. rollers, but piscivorous kingfishers face greater problems

since their prey are slippery and difficult to handle, as well as large. The long bill with its sharp tomia improves grip on fish. Kinetic coupling of the jaws appears to be reduced in the Alcedininae and some Cerylinae where the postorbital ligament is weak or absent; possibly this facilitates bringing the jaws parallel, giving maximum contact with prey. Jaw adductors are generally well developed, including a pinnate *M.pter.lat.* which is attached to the maxillo-palatine in the Alcedininae and Daceloninae and the whole head and bill is relatively massive, imparting the characteristic appearance of body form in kingfishers. Apart from the need for a large feeding apparatus to cope with large prey, the heavy head and bill probably also aid correct alignment when diving through water; terrestrial feeding kingfishers show reduced skull weight. Bill length is influenced by prey size, and by the depth at which prey is secured; ecological factors involved would repay close study, e.g. among Neotropical species in which Fry (1970a) noted a simple mathematical ratio between bill lengths of species occurring within the same area. The 'elongated' form of the skull, with pterygoids, palatines and jugals lying almost in one plane is another aspect showing adaptation to movement through water and consumption of fish; reduction or loss of *M. pseudotemporalis profundus* has, however, resulted from the associated reorientation of the quadrate. *Clytoceyx rex*, despite its extraordinary bill shape, shows the same basic skull morphology; this bizarre species would, nevertheless, be worth intensive study in the future, both in the field and the laboratory. A basiphenoid notch (Burton, 1978) present in all Cerylinae and many Alcedininae and Daceloninae, is believed to be a diving adaptation, perhaps related to Eustachian function.

The tongue (of only minor value in fish consumption) is much reduced, the basihyal expanded to form a wide, flat plate. *M. ceratohyoideus* is feeble, and *M. stylohyoideus* has an atypical insertion (anterior tip of ceratobranchiale). *M. branchiomandibularis* has an entirely mandibular insertion in the Alcedininae and Cerylinae, but is generally reduced in some smaller species. *M. hypoglossus* is feeble. The neck musculature shows remarkable development of head extensors, particularly *M. biventer* and *M. complexus*, providing the extra force needed to support or stabilize the heavy head when handling prey or diving.

Taxonomic problems within the family are for the most part at species or genus level, and anatomical studies are of limited value in resolving them; the basic division into three subfamilies is well supported by this study. The Cerylinae fall into two groups clearly separated by presence or absence of *M. pseudotemporalis profundus*. Lack of the muscle is obviously a derived character, possession a primitive one; however, those with the muscle appear to form a more closely related group, sharing generally large size and plumage similarities. Conversely, absence of the muscle may have been derived twice; Fry (pers. comm.) considers Neotropical forms (*Chloroceryle* spp.) probably not closely related to *Ceryle rudis*. The relationship of *Tanysiptera* to other Daceloninae may be worth further study; in skull form, and some features of jaw musculature (e.g. *M. pterygoideus lateralis*) it is atypical of the subfamily, and perhaps rather primitive.

TODIDAE

Todies feed on small flying insects close to fairly low foliage and their wide flat—yet long—bills, with strong rictal bristles obviously facilitate this. They are tiny birds and some of their structural features are no doubt related to small size. This is no doubt true of their general simplicity of jaw muscle structure, and especially the reduction of *M.add.mand.ext.rost.-temp.*—a feature of many small birds. Reduction or loss of *M. stylohyoideus* and possession of *M. hypoglossus obliquus* of Type 1 (alone among the families studied here) may also be size related phenomena. Some other features in the hyoid region are less easy to assess. The basihyal has lateral flanges unlike anything seen in other Coraciiformes or Piciformes, and *M. branchiomandibularis* has a unique strap like medial slip inserting on the mucosa.

There is a general resemblance to the Momotidae, though perhaps not detailed enough to provide firm support for the proposition that the two families are closely allied (see, e.g. Olson, 1976). However, there is certainly little similarity to the Alcedinidae beyond the features shared by all typical Coraciiformes. Sibley & Ahlquist (1972) suggested, on the basis

of egg-white protein studies, that todies were more closely related to kingfishers than to motmots. Structurally there is little to support this idea beyond a superficial resemblance in body form which has certainly been imposed by quite different functional needs.

MOMOTIDAE

Motmots feed among foliage or from the ground, often on fairly large prey. Foraging tactics may include both waiting on a vantage point and active search, sometimes on the ground. In broad features, such feeding behaviour resembles that of some kingfishers, rollers and even puffbirds, but they show distinctive structural features, most obviously the serrated tomia of the bill. This no doubt provides improved grip on prey, but it is not clear why this feature is absent in other birds (particularly Coraciiform ones) with similar feeding habits. Perhaps the serrations appeared as the result of some relatively rare genetic change which has simply failed to occur in most groups. Alternatively, it may be related to specific needs, and a closer study of diet may shed light on these. Soft bodied yet powerful prey such as the Tettigonidae which abound in Neotropical forests might be best handled with serrated bill edges. The extraordinary broad bill of *Electron* provides a further puzzle, and its feeding methods reveal no simple answer; again, a more thorough knowledge of diet may be helpful.

Jaw muscle features agree closely with the general characteristics of the typical Coraciiformes. M.pter.lat. is bipinnate only in *Momotus* and *Baryphthengus*, correlating with generally better developed jaw musculature and more robust bills than in *Electron*. The tongue is long and more or less brush tipped, as in rollers. M. stylohyoideus is present, but inserted posteriorly on the basihyal, and the origin of M. branchiomandibularis is variable—on the mandible, or mucosa, or both. M. genioglossus is present. Neck muscle structure shows no unusual features.

It is unfortunate that no specimens of *Hylomanes* were available for study, and that so little is known about the habits of this bird. Although much larger, it certainly shows some approach to the Todidae in bill and body form, and may be able to shed some light on the origin of the Todies.

MEROPIDAE

The long bills of bee-eaters are a vital safeguard against the stings of the venomous insects on which they often feed, but an unusual feature amongst aerial insect hunters in general. Only the Galbulidae resemble them in this way, and for the same reasons; most birds which capture flying insects have large gapes with wide and often very short bills. The problem of accurately seizing a flying insect with a long narrow bill must be considerable, and elucidation of the adaptations needed to overcome them would make an interesting study. More detailed discussion of this topic as it concerns the Galbulidae is provided by Burton (1977a).

Nyctiornis spp. are larger and less aerial bee-eaters which differ from other Meropidae in their relatively shorter but more robust bill, generally more massive jaw musculature, and, interestingly, the lack of Mm. pygmaei. Other bee-eaters show general uniformity of feeding apparatus structure with no significant differences between smaller species which hunt from a perch, and larger ones feeding in continuous flight.

Bee-eaters have broad skulls with a wide occipital region, providing a large moment arm for neck muscles concerned with stabilizing or moving the head. This may be of importance during aerial pursuit, and certainly for the vigorous movements needed to kill and de-venom prey. The postorbital ligament is slender, M.add.mand.ext.rost.temp. is long but very narrow, and M.add.mand.ext.rost.lat. is vestigial. The tongue is long, with a slight brush tip, and M. branchiomandibularis originates on the ventral surface of the buccal mucosa. M. genioglossus and M. ceratoglossus anterior are present.

Bee-eaters and jacamars show many structural resemblances (Fry, 1970b) as might be expected from their similar ways of life. Skull form is similar, and M.pter.lat. is markedly narrow in both families—vestigial in some Galbulidae. Both groups (except *Nyctiornis* among the Meropidae) possess a well developed set of M. pygmaei. M. hypoglossus medialis is found only in these two families and the Bucconidae; exactly what this common feature denotes is hard to surmise, however. Many of the resemblances between these two families

are, no doubt, due to convergence. However, their origins may not be quite as distant as present classification would suggest—a point which is discussed at length elsewhere in this review.

LEPTOSOMATIDAE

The Cuckoo-roller, *Leptosomus discolor*, resembles *Coracias* spp. in general features of body form and habits, but detailed examination reveals many differences, as Cracraft (1971) found in his osteological study. It is unquestionably correct to classify it in a monotypic family, but rather harder to understand the significance of all its distinctive features. *Leptosomus* evidently originated from an early invasion of Madagascar, well before that which gave rise to the ground rollers, and it certainly retains some primitive features—for example, *M. stylohyoideus* is present and *M. branchi mandibularis* unspecialized. However, *Leptosomus* also shows structural modifications which are derived, and in some cases unique. *M.add.mand.ext.rost.temp.* is surprisingly small, and lacks bipinnate structure; *M.add.mand.ext.vent.* has aponeurotic attachment to the stout postorbital ligament; *M.add.mand.ext.caud.* has only one raphe; *M.pseud.superf.* has a reduced lateral origin. As in the *Coraciidae*, *M.pter.dors.med.* is subdivided into anterior and posterior portions, but in *Leptosomus* the anterior portion is much reduced. *M.pseud.prof.* has a lateral slip merging with the insertion of *M.pseud.superf.*; despite the presence of *M. stylohyoideus* there is an additional slip resembling it from *M.serpiphyoideus*; the tongue is short and lacks any indication of a brush tip.

There are no obvious behavioural factors to account for these features. The Cuckoo-roller's regular consumption of chamaeleons is certainly unusual, but these would hardly seem to require different adaptations from *Coracias* which also feeds on lizards, though of other kinds. The peculiarities of *Leptosomus* may well be associated in some way with its long isolation under conditions of reduced competition and ecological diversity, but much further study will be needed to understand them fully. Further comments on its systematic position will be found in the section on the Galbuloidea.

CORACIIDAE

Ground rollers have been included here, following Peters (1945), but there are good grounds for separating them as a distinct family *Brachypteraciidae* (Cracraft 1971; Morony, Bock & Farrand, 1976). Reasons for doing so stem, however, from differences in behaviour, plumage and post-cranial anatomy; as Cracraft (1971) found, cranial osteology is very similar throughout, and the present study reinforces his observations.

Eurystomus is the most divergent genus in feeding apparatus structure, with its wide bill and gape adapted for aerial feeding. However, even here, differences are mainly ones of proportion, and in essential features it is very similar to *Coracias* and the ground rollers. All rollers have robust skulls, with very stout postorbital ligament and well developed medial brace. *M.add.mand.ext.rost.temp.* is large, but *M.a.m.e.r.lat.* is small or absent, and *M.pter.lat.* is fairly broad, but of simple structure. *M.pter.dors.med.* shows division into distinct anterior and posterior portions. Although some large prey, such as lizards, is taken and swallowed whole, there is still clearly a need for effective tongue action in dealing with smaller items, since tongues are relatively long with brush tips, especially in ground rollers. A curious feature of hyoid anatomy is the lack of a true *M.stylohyoideus*, the slip which replaces it being derived apparently from *M. serpihyoideus*; the *Galbulidae* and *Bucconidae* are the only other families showing this character, although the slip from *M. serpihyoideus* is present in the *Leptosomatidae*. *M. branchi mandibularis* originates mainly on the mucosa. *M. genioglossus* is present in ground rollers. *Mm. pygmaei* were found in *Coracias* and *Eurystomus*.

Hoopoes, Wood-hoopoes and Hornbills

Although agreeing with the typical *Coraciiformes* in some important ways, these three families have many distinctive features of their own in feeding apparatus structure, and

appear to constitute a well-marked natural group. The idea of such a relationship has a long, if chequered, history, dating back to Murie (1873), and receives some support from the egg-white protein studies of Sibley & Ahlquist (1972). Some of the shared features appear to be primitive, but undoubtedly most are derived ones associated with specialized methods of using the bill. Most sophisticated of these methods is 'gaping', i.e. opening the bill within a substrate to create a cavity permitting access to concealed prey. This technique is well known in various birds of other groups, e.g. Icteridae (Beecher, 1951), Callaeidae (Burton, 1974). In the present study the Phoeniculidae and Upupidae show the same characteristic gaping adaptations—a long retroarticular process, and massive *M. depressor* and *M. protractor*. Of the three families, the Phoeniculidae is the only one to show narrowing of the skull anterior to the orbit sufficient to permit a useful view between the open jaws as in *Sturnus* (Lorenz, 1949). Lack of this feature in *Upupa* may be an unavoidable mechanical necessity to provide an adequate brace against forces acting laterally against the very long bill, when probing hard soil. The Bucerotidae, which feed to a large extent on fruit and exposed animal prey, make less use of this technique, but it is certainly used in foraging by some species, and perhaps also in nest excavation; there is generally at least an indication of a retroarticular process, even though *M. depressor* and *M. protractor* are not greatly enlarged. Probably the Bucerotidae arose from a stock in which some specialization for gaping and vigorous excavation had already appeared; the Upupidae and Phoeniculidae seem likely to have shared the same ancestry, but diverged later from a group which had carried this specialization a good deal further. Within the Bucerotidae (q.v.), other forms of bill use have appeared, also leading to drastic structural change.

The skull is robust and heavily ossified in all three families, even apart from the Bucerotidae. The postorbital ligament is moderately to very strongly developed, and the occipito-mandibular ligament unusually stout. However, a medial brace is lacking or only weakly developed (Upupidae). The maxillo-palatine bridge is complete, and is fused with the palatines in the Bucerotidae. The medial condyle of the quadrate is not especially prominent.

M. adductor mandibulae externus is of complex structure in the Phoeniculidae; reasons have been advanced elsewhere (p. 408) for considering this structure primitive. In the Upupidae and Bucerotidae, simplified traces of this structure remain. *M. pseudotemporalis superficialis* departs from the condition seen in the typical Coraciiformes; although its lateral origin is well developed, it is much more bulky in the dorso-ventral plane, so that the trigeminal nerve is deeply buried. This condition is more normal among birds in general, and hence can be considered more primitive than in typical Coraciiformes, or even the Trogoniformes (see p. 437).

Within the three families, an interesting situation exists with regard to *M. pterygoideus dorsalis*. The muscle shows no division into lateral and medial portions in the Upupidae or Phoeniculidae (although bipinnate in *Phoeniculus purpureus*), while in the Bucerotidae it is divided, but in a different position, relative to *N. pterygoideus*, from any other Coraciiformes or Piciformes. This suggests that the undivided condition is primitive, and that division has occurred independently in the Bucerotidae. Attachment to the maxillo-palatine is found in the Phoeniculidae and Bucerotidae.

In all three families a retractor palatini portion is developed from the medial region of *M. pterygoideus dorsalis*. Attaching on the base of the cranium, it acts to depress the lower jaw without at the same time raising the upper. This probably improves control in the manipulation of food objects—probably an important facility for birds with long bills and short tongues. Kinetic coupling of jaw action is evidently possible, with a well developed postorbital ligament, but it is interesting that *Bucorvus* also shows jaw coupling by means of the structure of the quadrate/mandible articulation. This system is permanent, not depending (as with the ligament) on its state of loading. Whether, and how this relates to the strongly predatory habits of the Ground Hornbills, is a matter for conjecture.

Tongue reduction is most extreme in the Upupidae; the Phoeniculidae and Bucerotidae have rather longer tongues rendered distinctive by the numerous barbs in the basal region.

In all three families, the basihyal has a distinctive 'hour-glass' shape. The origin of *M. branchiomandibularis* is entirely on the mandible, but far anterior. *M. genioglossus* is present in all three families, with left and right muscles partly or entirely united in the midline. *M. hypoglossus obliquus* resembles that in some typical Picidae, with entirely separate left and right sides, and origin on the ceratobranchiale in the Upupidae and Phoeniculidae. *M. tracheohyoideus* has origin on the clavicle, and on the sternum also in the Bucerotidae.

UPUPIDAE

There is a moderately developed postorbital ligament and a weakly developed medial brace. The orbital process of the quadrate is narrower than in the typical Coraciiformes, but broadened at its tip; vestigial basiptyergoid processes are well marked. The postorbital and zygomatic processes lie unusually close together, and in consequence *M.a.m.e.rost.temp.* is small and narrow. *M.a.m.e.* has a well developed postorbital lobe, but in structure is otherwise fairly similar to that of the typical Coraciiformes, with small *M.a.m.e.rost.lat.*, *M.a.m.e.vent.* with a wide fleshy insertion on the lateral surface of the mandible and a narrowly inserting *M.a.m.e.caud.* *M.pter.dors* is undivided and of simple structure, with *N. pterygoideus* entering it well posteriorly.

The tongue is extremely short, without basal barbs. Tongue reduction would seem to be inevitable, since the bill lacks any lumen, for most of its length, in which a tongue could operate. This is a consequence of the reinforcement needed for jaws which are used to probe the ground; a similar effect is seen in various other birds which probe hard substrates, e.g. *Numenius* (Burton, 1974). *M. stylohyoideus* is extremely slender, and the right and left *Mm. genioglossi* are completely united as a single median muscle. Rather surprisingly, *M. splenius capitis* has only the usual origin on 2; forceful head movements when probing might have been expected to require extra attachment on 3 as in the Phoeniculidae. The weak *M. biverter* is also somewhat surprising. There is obviously still a need for detailed observations on feeding techniques in this common and widely distributed bird.

PHOENICULIDAE

The skull is very similar in general form to that of the Upupidae, particularly in *Phoeniculus*. *Rhinopomastus* has a less robust skull and strongly decurved bill, probably relying less on gaping, and more on the exploration of insect tunnels. The orbital process of the quadrate is rather more slender, and the palatines wider. There is no medial brace. As in the Upupidae, the postorbital and zygomatic processes are close together, with consequent reduction of *M.a.m.e.rost.temp.* Otherwise, *M.a.m.e.* is of the complex structure postulated as primitive, with a two part postorbital lobe, narrowly inserting *M.a.m.e.vent.*, and a large, laterally expanded *m.a.m.e.caud.* *M.pter.dors.* is undivided, (bipinnate in *Phoeniculus purpureus*) and is attached to the maxillo-palatine.

The tongue shows less extreme reduction than in the Upupidae, and is relatively quite long in *P. aterrimus*; probably it is helpful in transporting such prey as beetle grubs back to the mouth while probing wood. The tongue base is studded with barbs, *M. stylohyoideus* is normally developed, and *M. hypoglossus obliquus* particularly well developed, its origin extending well back on the ceratobranchiale. Left and right *Mm. genioglossi* are united only anteriorly. *M. splenius capitis* has additional origin on the neural spine of vertebra 3—an adaptation for forceful lateral head movements while probing.

The marked differences in bill shape within the family make them an attractive potential subject for a comparative study of feeding behaviour, with which *Upupa* could well be included.

BUCEROTIDAE

The bills of the Bucerotidae are, of course, their most distinctive feature. Long and deep, their shape is well suited to fruit eating, combining adequate reach with the rigidity needed to support heavy objects at the bill tip. A variety of functions other than feeding are also served by the bills of these birds. Their laterally flattened shape renders them suitable for use as a spatula in applying mud to the nest hole, or for splitting off rotten wood where

necessary. Adornments of the bill and casque probably serve as species specific social signals, and the bill of the walled-up female may have significant value in intimidating predators at the nest hole. Normally highly pneumatized, the casque is solid in *Rhinoplax*—probably a secondary adaptation providing extra weight to aid in excavation.

Tockus spp. appear the least specialized, and perhaps the most primitive hornbills. Their skulls, though more massive, are not unlike those of *Phoeniculus* spp.; in larger, heavily casqued hornbills, the resemblance is less obvious. Principal differences apart from bill and casque are the extensive temporal fossa, and the fusion of the maxillo-palatine bridge with the anterior part of the palatines. The quadrate is more robust, and more like that of typical Coraciiformes, with stout orbital process and prominent (though more rounded) medial condyle. The postorbital ligament is extremely broad and strong; coupled kinesis, achieved when the ligament is loaded, is probably essential for the deft throwing and catching movements of which hornbills are capable. They are also able to perform remarkably fine manipulation with the bill-tip, for which independent jaw action would seem important; the retractor palatini portion of *M. pterygoideus* may be of special value in allowing force to be exerted on the upper jaw alone. However, *Bucorvus* has the jaws coupled not only by the postorbital ligament, but by the structure of the quadrate/mandible hinge, and would seem scarcely capable of uncoupled kinesis; nevertheless, it can carefully manipulate prey, and has a bulky retractor palatini.

Powerful adduction is important, for heavy objects may often need to be grasped securely at the bill tip, and some species systematically crush venomous prey. The extensive *M.a.m.e. rostr.temp.* is largely responsible for the force developed by *M.a.m.ext.*, since fleshy insertion on the lateral surface of the mandible is almost eliminated, though Aponeuroses 1 and 3 are very strong. A small postorbital lobe only remains from the primitive form of the muscle seen in the Phoeniculidae. *M. pseudotemporalis profundus* has bipinnate structure—an unusual feature among birds in general, but perhaps providing more force than a parallel-fibred muscle for small amplitude coupled jaw movements occurring in throwing and catching actions. *M. pter.dors.* is divided, but well anterior to the point of entry of *N. pterygoideus*. *M. pter.lat.* is bipinnate, with extensive attachment to the maxillopalatine, and the retractor palatini portion of *M. pter.dors. med.* is also bipinnate.

The tongue is relatively short, but well developed, and much barbed at its base. *M. stylohyoideus* is absent. The origin of *M. branchiomandibularis* is a median one at the mandibular symphysis, where right and left muscles meet. Left and right *Mm. genioglossi* are completely united. *M. splenius capitis* had additional origin on vertebra 3. The extra force this provides for head raising or turning is of obvious value for birds which handle substantial objects deftly but powerfully with massive heads.

It is unfortunate that no spirit specimen of *Rhinoplax vigil* exists. A study of the jaw musculature would valuably supplement the work of Manger Cats-Kuenen (1961), while the neck musculature may well show unusual modification for support of the extraordinarily heavy head. In general, there is a need for a more comprehensive study of the feeding apparatus in the Bucerotidae, to extend the work of Starck (1940) and the present investigation, both of which have dissected relatively few species.

Jacamars and Puffbirds

These two families at present constitute the suborder Galbuloidea of the Piciformes. The most thorough anatomical study supporting this placement is that of J. Steinbacher (1937), though this dealt rather briefly with the Coraciiformes. More recently, Verheyen (1955b) retained them in this systematic position after a study of skeletal measurements. However, the present investigation casts very serious doubt on this classification, for in almost every aspect of feeding apparatus structure they share important characters with the typical Coraciiformes and virtually none with other Piciformes. This evidence agrees with the findings of Sibley & Ahlquist (1972) from egg-white protein studies. Common features of the Galbuloidea and the typical Coraciiformes may be summarized as follows:

1. Desmognathous palate.
2. Quadrate with deep and prominent medial condyle, and a broad orbital process having a long medial edge for attachment of the aponeurosis of *M.pseud.prof.*
3. *M.add.mand.ext.* having no *M.a.m.e.r.lat.*, an *M.a.m.e.vent.* which fans out well anteriorly, and an *Ap. 3a* in *M.a.m.e.caud.*
4. The condition of *M.pseud.superf.*, which is thin, originating rather high in the orbit, and with its fleshy portion lying mainly lateral to NV. A reduced muscle in many *Coraciiformes*, it is vestigial in the *Galbuloidea* and even absent in a few.
5. The largely cartilaginous entoglossum.
6. Very short basihyal.
7. *M. branchiomandibularis* originating far forward on the mandible, and often with additional origin on the ventral side of the buccal mucosa.
8. *M. tracheohyoideus* with origin on the clavicle.
9. The presence of *Mm. pygmaei* in some species.

With the exception of 9, probably all these features can be correctly regarded as derived ones. In addition, the *Galbuloidea* share two features with individual *Coraciiform* families; *M. stylohyoideus* is functionally replaced by a slip from *M. serpihyoideus* as in the *Coraciidae*, and *M. hypoglossus medialis* is present as in the *Meropidae*. (It may be noted here that *Leptosomus* possesses both the slip from *M. serpihy.* and an *M.stylohy.*, and also has a well developed *M. ceratoglossus anterior*, from which *M.hyp.med.* is probably derived.) The only feature of any note in which the *Galbuloidea* agree with the typical *Piciformes* is in their lack of a medial brace providing secondary articulation for the lower jaw; however *Leptosomus* among the typical *Coraciiformes* also lacks a medial brace.

Despite this evidence conflicting with their present ordinal classification, many characteristics attest to a fairly close affinity between the *Galbulidae* and *Bucconidae* themselves. The very long postorbital process and extremely deep medial quadrate condyle lend their skulls a characteristic appearance posterior to the orbit (though resembling the *Coraciidae* and *Leptosomatidae*); the great reduction or even loss of *M.pseud.superf.* is very striking, taking a typical *Coraciiform* trend to its extreme; origin of *M. branchiomandibularis* from the mandibular symphysis is otherwise seen only in the *Bucerotidae*, which are surely only distantly related; the *Bucconidae* and some *Galbulidae* have a narrow median groove on the dorsal surface of the tongue unlike anything seen in other families studied; and the replacement of *M. stylohyoideus* by a slip of *M. serpihyoideus*, and presence of *M. hypoglossus medialis* are features otherwise seen only in single families of typical *Coraciiformes*.

Exactly how the two families arose is a matter for conjecture. The puffbird body form and way of life is almost certainly the more primitive, but no living puffbird appears much like a potential jacamar ancestor. *Chelidoptera* is an aerial feeding puffbird, but its similarity to jacamars in way of life is a secondary and rather superficial one (Burton, 1977a). Delving further back, it is interesting to note features shared by the *Galbuloidea*, *Coraciidae* and *Leptosomatidae*. *Leptosomus* is particularly intriguing. Apart from some jaw muscle peculiarities of its own, it shows many similarities to puffbirds, even to its partially zygodactyl feet; had it occurred in South America rather than Madagascar, its present classification might have been very different. I would suggest, tentatively, that the *Galbuloidea* arose from a stock not far removed from that which gave rise to the rollers and cuckoo-rollers. The position of this group of families relative to other typical *Coraciiformes* is less clear, and is discussed further in the concluding section on phylogeny.

GALBULIDAE

The long, straight, pointed bill is the most obvious structural characteristic distinguishing jacamars from puffbirds. Its purpose (as in the *Meropidae*) is undoubtedly to protect vulnerable parts of the head from the stings of venomous insects. The skull is less robust, but with a characteristic profile; the occipital region bulges upwards and posteriorly, and the elements of the kinetic apparatus lie in one plane with the upper jaw, rather as in the elongated skulls of kingfishers though with a normally sited quadrate. As in the *Meropidae*, whose skulls are

similarly shaped, the form of the cranium may be related to the resting attitude with upward pointing bill while waiting for insects.

Suppression of M.pter.dors.lat. is much more extreme than in the *Bucconidae*, but in *Jacamerops* a partial secondary division of M.pter.dors.med. has appeared. The tongue is long, with slight indication of a brush tip in *Jacamerops*. There is no M. genioglossus. M. splenius capitis is unusually large in the *Galbulidae*, covering most of the very broad occipital region of the skull. Its role during pursuit of aerial prey is discussed by (1977a).

Jacamars are highly uniform in structure; the only aberrant species are *Galbalcyrhynchus leucotis* with its extremely heavy bill, and the large *Jacamerops aurea*, with a comparatively short and heavy bill. Little is known about the former, and its feeding habits certainly deserve study, to clarify the factors underlying its unusual bill form. *Jacamerops* is less aerial than other jacamars, its habits somewhat resembling those of a puffbird. Nevertheless, detailed structure of its feeding apparatus so closely resembles that of others of its family that it seems almost certain that its atypical features are secondary ones. In this it differs from *Nyctiornis*, which is a rough ecological equivalent among bee-eaters, but seems to have diverged early in the history of the *Meropidae*.

BUCCONIDAE

Puffbirds are more variable in bill form, size and habits than the jacamars, but invariably more sluggish, feeding on the whole less frequently, though often on larger prey. Even the small and highly aerial *Chelidoptera* conforms to this general rule (Burton, 1977a). Skulls are generally more robust, and more normal in form. M.pter.dors.lat. varies considerably in size relative to M.pter.dors.med., but is generally larger than in the *Galbulidae*. The tongue is of moderate length, simple in shape, and with a very strongly marked median dorsal groove. M. genioglossus is present, left and right muscles having a combined origin on the myophysis.

As stated earlier, no living puffbirds give much indication as to the likely origin of the jacamars, and *Chelidoptera*, despite its aerial habits, seems an unlikely candidate for an ancestral form. Small, lower storey flycatcher/gleaner types such as *Nonnula* or *Micromonacha* may be somewhat nearer to the type of bird from which the *Galbulidae* were derived.

Typical Piciformes

With the *Galbuloidea* removed, the remaining families of *Piciformes* form a closely knit and clearly natural group. Differing in numerous ways from the *Galbuloidea* and *Coraciiformes*, they share many derived characters of feeding apparatus structure, some of which reach an extreme in the pecking and tongue probing adaptations of the *Picidae*. Somewhat surprisingly perhaps, the *Picidae* also stand out by reason of the primitive structure of M.add.mand.ext., which they alone retain.

Typical *Piciformes* have a quadrate with a long and rather slender orbital process, and a medial condyle which is not especially prominent. None of them possess a medial brace providing secondary articulation for the lower jaw. In the *Picidae* (including *Jynx*) and *Indicatoridae*, the junction of pterygoid and palatine has a distinctive form, with the pterygoid extended far anteriorly medial to the palatine, so that the two bones have a large area of contact—an arrangement seen in many passerines, but none other among the *Coraciiform/Piciform* assemblage. Characteristic features of M.add.mand.ext. seen in the *Capitonidae*, *Indicatoridae*, *Ramphastidae* and *Jynx* include the extensive M.a.m.e.rost.lat., which spreads out ventrally as a wide, thin sheet covering much of M.a.m.e.vent., which itself fans out quite close to the origin. M.a.m.e.caud. usually lacks an Ap. 3a. M.pseud.superf. lacks any lateral lobe, and is situated well into the orbit with the fifth cranial nerve running entirely lateral to it, deeper than in typical *Coraciiformes* and the *Galbuloidea*. It often has a medial extension at the origin, overlapping part of M. protractor. M.pter.dors.lat. is usually well developed, with attachment to the maxillo-palatine in the *Ramphastidae* and a few *Capitonidae*. (Where this attachment is well developed, it is made by a distinct dorsal slip from the

muscle, not seen in the Coraciiformes). *M. pter. dors. lat.* is bipinnate in the Picidae. The Picidae, other than *Jynx*, also exhibit a greatly enlarged *M. protractor*.

Tongues are generally well developed, and the basihyal is usually a long and fairly slender rod. An extreme is reached in the Picidae where the tongue itself is much reduced, but extended on an enormously lengthened basihyal. Nearly all, other than the Picidae, have an entoglossum of highly characteristic form, with a constriction about half way along its length. It is entirely ossified in some, while in others, the constricted region is cartilaginous, with the anterior ossified region having the form almost of a second entoglossum in front of the first. *M. branchiomandibularis* originates on the medial surface of the mandible, not far forward—the condition characteristic of most birds. *M. hypoglossus obliquus* is long, often with origin on the ceratobranchiale, reaching an extreme in the Picidae. *M. tracheohyoideus* originates on the anterior tip of the keel of the sternum, or the clavicular symphysis, right and left muscles meeting at the narrow point of origin—not separate origins more laterally on the clavicle as in the Coraciiformes and Galbuloidea. *M. pygmaei* have not been found in any of the typical Piciformes.

Functional or taxonomic problems within the group are best dealt with at family level. As a general comment however, it is worth stressing the significance of tongue action within this group. Tongue manipulation, sometimes in combination with various forms of excavation, has clearly been a major factor in the evolution of feeding specializations within the typical Piciformes. Although tongue movements are extremely difficult to observe and study, the attempt needs to be made if we are ever to understand how their various feeding mechanisms arose.

CAPITONIDAE

Barbets are the least specialized family of Piciformes, yet they show some interesting modifications of feeding apparatus structure that suggest possible ways in which the more extreme specializations of other families originated. For this reason they certainly deserve much closer study.

Fruits predominate in their diets, and their wide, ample bills, sometimes with serrated or notched tomia, are primarily adapted for seizing and gripping them. Barbets all lack a post-orbital ligament, though some capacity for coupled jaw action by means of a modified quadrate/mandible hinge seems to exist in *Megalaima*. Independent jaw action may be important where several fruits have to be carried simultaneously (as illustrated in Thomson, 1964). Some are weakly desmognathous.

M. add. mand. ext. conforms closely to the structure characteristic of the typical Piciformes; *M. a. m. e. r. temp.* is usually extensive, reaching back nearly to the skull midline. *M. pseud. superf.* has a medial extension at the origin, generally partially overlapping *M. protractor*, and is bipinnate in some species, sometimes with a distinct bipinnate medial slip. *M. pter. dors. lat.* is usually extensive, and has attachment to the maxillo-palatine in several species. In *Semnornis*, this attachment takes the form of a distinct and well developed dorsal slip.

The tongue is moderately long, simple in form in most, but with a brush tip in *Capito* and *Semnornis*. Double structure of the entoglossum is generally well marked, though absent in *Lybius bidentatus*. The basihyal is long except in *Pogoniulus*. *M. hypoglossus obliquus* is also long, though its origin extends onto the ceratobranchiale only in *Pogoniulus*, perhaps in compensation for the short basihyal.

INDICATORIDAE

With their sober plumage, unspecialized bills and horizontal carriage, honeyguides look more like typical passerines than members of the Piciformes. Nevertheless, in feeding apparatus structure they are closely similar to barbets. The skull is less robust, with reduced ossification particularly apparent in the vomer, maxillo-palatines and upper jaw; there is, however, a weak postorbital ligament. Presumably a heavily reinforced skull is unnecessary to cope with a diet of bee grubs and honeycomb.

M. add. mand. ext. is closely similar to that of barbets, with *M. a. m. e. rost. lat.* expanded across *M. a. m. e. vent.* as a thin sheet of fibres. *M. a. m. e. rost. temp.* is moderately developed,

M.a.m.e.caud. only weakly pinnate. M.pseud.superf. has a long medial extension at the origin, and is bipinnate in some. M.pter.dors.lat. is bipinnate in some honeyguides, but is not attached to the maxillo-palatines.

The tongue is simple in structure, and moderately long. The entoglossum is constricted at about the middle of its length, with a cartilaginous middle region and ossified tip. The basihyal is fairly short, but M. hypoglossus obliquus very long, its origin extending to the posterior end of the ceratobranchiale as in the Picidae.

Sibley & Ahlquist (1972) suggested on the basis of egg-white protein studies that the possibility of affinity between honeyguides and cuckoos should be investigated. It must therefore be emphasized that the findings of this study provide strong evidence against any such affinity. I have examined feeding apparatus anatomy in a variety of Cuculiformes, and find it to differ extensively from that of honeyguides. On the other hand, the detailed similarities between honeyguides and other typical Piciformes are hard to discount; indeed, judged on some features of palate structure and the much elongated M.hyp.obl., the Indicatoridae may hold the key to understanding the origin of the Picidae (q.v.)

It may be remarked here that *Prodotiscus* spp. differ markedly from other Honeyguides in bill form and, probably, ecology. Unfortunately, study of their anatomy is much hampered by the present lack of anatomical specimens in museum collections. Remedy of this deficiency might lead to a substantial improvement in our understanding of the evolutionary history of the Piciform families.

RAMPHASTIDAE

The most obvious characteristic of toucans is, of course, the huge bill. This seems primarily adaptive to fruit eating, though as with the Bucerotidae, it has acquired secondary signal functions. The mechanism of feeding, however, clearly differs substantially from that of hornbills, since there is no post-orbital ligament (as in barbets), nor any form of kinetic coupling by modification of the quadrate/mandible articulation. Moreover, the tongue, far from being reduced, is very long, with brush tip and edges. Unfortunately, there is insufficient information about the feeding habits of toucans to interpret these facts satisfactorily. It is not known whether, for instance, toucans regularly hold several fruits along the length of the bill—an action for which reduced coupling might be helpful. Fruits are swallowed whole, and use of the tongue does not appear vital for this purpose; however, insects also figure in the diet, especially when young are being fed, and the tongue may then have some important part to play. Swainson's Aracari is recorded as eating flower filaments; the tongue seems well suited for transporting these along the bill, but how widespread the habit may be is unknown.

Bill shape, a doubly desmognathous palate and lack of a vomer distinguish toucan skulls from those of barbets. Otherwise, they are extremely similar, as is the jaw musculature. M.a.m.e.rost.temp. extends less far back in the Ramphastidae, but otherwise differs negligibly from that of the Capitonidae. M.pseud.superf. is of similar form to that of barbets, but is rather more bulky, and bipinnate in all species examined. M.pter.dors.lat. is attached to the maxillo-palatine by a distinct and bulky dorsal slip.

Despite the longer tongue, the entoglossum is very much like that of some barbets, with similar double structure and a narrow midpoint cartilaginous zone. There is a vestigial M. genioglossus in *Selenidera*. M. hypoglossus obliquus is long, its origin including the anterior part of the ceratobranchiale.

The findings of this study leave little room for doubt that the Ramphastidae and Capitonidae are closely related. I see no need even to postulate a common ancestor for the two families; it seems reasonable simply to regard toucans as a specialized group of barbets which have arisen and radiated in South America. They may well be no further removed from the main stem of barbet evolution than, say, *Pogoniulus*. This is not necessarily, however, to advocate merging the two families; the appearance of such a striking innovation as the toucan bill surely requires taxonomic recognition, though perhaps this might be more

appropriately at subfamilial level. However, they are for the present retained as a family in the classification proposed at the end of this paper.

The further question arises as to which barbet group might have given rise to the toucans, and it seems that the answer may well lie in their own zoogeographical region. *Capito* and *Semnornis* of the Neotropics are the only barbets in which brush tongues were found, and *Semnornis* shows additional significant resemblances. It possesses an M.pter.dors.lat. in which attachment to the maxillo-palatine is made by a distinct dorsal slip, just as in the Ramphastidae. Furthermore, *S. ramphastinus* shows a striking similarity in colour pattern to some species of *Andigena* and *Selinidera*, while even the plain coloured *S. frantzii* is not unlike *Bailloni* *bailloni*. Detailed studies of these birds, particularly in the field of behaviour, should produce results of great interest.

PICIDAE

Woodpeckers (Picinae) and piculet (Picumninae) share many highly distinctive structural features, mostly adaptive to the excavation of wood by hammering. Wrynecks (Jynginae), by contrast, lack nearly all of these though all three have a similar highly modified tongue apparatus. This great disparity between Wrynecks and others makes it necessary to enumerate features point by point for the sake of clarity.

1. The skull of *Jynx* is in general unspecialized and light in structure, resembling that of *Indicator*, though showing even more reduction in the palatal region with vestigial vomer and narrowed maxillo-palatines. Other Picidae retain a simplified palatal structure, but the skull is otherwise heavily ossified, with specialized fronto-nasal hinge, pterygoids, quadrate and otic region. Wrynecks and woodpeckers share with honeyguides a distinctive structure of the pterygo-palatine junction.

2. The postorbital ligament is weak in *Jynx*, fairly strong in other Picidae.

3. The Picinae (but not Jynginae or Picumninae) have a forwardly directed spur from the lateral edge of the auditory capsule, with ligamentous connection (opisthotic ligament) to the quadrate.

4. In *Jynx*, M.a.m.e.rost.temp. is very small; otherwise, M.add.mand.ext. much resembles that of barbets and honeyguides, with M.a.m.e.rost.lat. expanded across M.a.m.e.vent. As in *Indicator*, Ap. 4 is scarcely detectable. In all other Picidae, the muscle is characterized by retention of presumed primitive features, particularly the narrow M.a.m.e.vent., and wide lateral expansion of M.a.m.e.caud.; M.a.m.e.rost.lat. also remains narrow.

5. M.pseud.superf. in *Jynx* has a medial extension of the origin as in barbets and honeyguides. In other Picidae, the muscle has a simple triangular shape, with no medial extension.

6. M.pter.dors.lat. is of normal shape and simple structure in *Jynx*; in other Picidae it is much elongated, and has bipinnate structure.

7. M. protractor is a narrow small muscle in *Jynx*, with no obvious subdivision or attachment to the orbital process of the quadrate. It is greatly enlarged in other Picidae, and consists of two distinct parts. There is extensive attachment on the orbital process, and the region of insertion on the pterygoid is developed as a long bony spur.

8. The tongue is unbarbed in *Jynx*, barbed in other Picidae.

9. Hyoid skeleton and musculature are very similar in all Picidae, including *Jynx*. Their many specialized features include a unique and distinctive muscle, M. geniothyreoideus (perhaps derived from M. geniohyoideus) and a greatly elongated M. hypoglossus obliquus (=M. ceratoglossus superior, Leiber), taking to an extreme the trend seen in other typical Piciformes, especially the Indicatoridae.

10. M. biventer is strongly developed in *Jynx*, weakly in other Picidae.

11. M. longus colli consists entirely of long slips in all Picidae, as also in the Indicatoridae. In *Jynx* (as in honeyguides), these are largely fleshy, but in other Picidae, the insertions of the muscle are made by very strong tendons, fleshy regions being confined to the slips of origin on posterior vertebrae.

It will be clear from this resumé that the central problem in understanding the evolution of the Picidae concerns the origin of the Jynginae. Though endowed with a specialized tongue apparatus very similar to that of woodpeckers, wrynecks totally lack their specializations for excavation, but show a derived condition of *M.add.mand.ext.* very similar to that of barbets and honeyguides. Obviously, then, either the tongue modifications or those of *M.add.mand.ext.* arose separately in the Jynginae—or, just conceivably, both. The specialized features of tongue, hyoid and hyoid musculature are numerous, and include the appearance of a muscle (*M. geniothyreoideus*) apparently unique to the family. On balance, therefore, it seems reasonable to regard the Jynginae as a group which diverged early from woodpecker stock at a stage when tongue modifications had appeared, but not specializations for hammering. If this view is correct, then the structure of *M.add.mand.ext.* in *Jynx* was derived separately from that in barbets and honeyguides, resemblances being due, perhaps, to similar genetic potential in these groups.

However, the alternative possibility should not be discounted; if wrynecks arose from an early honeyguide/barbet stock, then their jaw muscle similarities would be due to common origin, and the woodpecker-like tongue apparatus must have evolved separately in wrynecks. This is not impossible; the basis for the woodpecker tongue (e.g. long basihyal, very long *M. hypoglossus obliquus*) already exists in barbets and honeyguides, and only the rather mysterious *M. geniothyreoideus* would require to be explained. Similarities of palate structure between wrynecks and woodpeckers are probably of minor significance. It would not take much more reduction of ossification in honeyguides to leave vomer and maxillo-palatine vestiges like those of the Picidae; indeed *Prodotiscus* spp. may well prove to have such structure if and when anatomical specimens are ever obtained. It is interesting to note, however, that woodpeckers and piculets clearly went through a wryneck-like phase with reduced skull ossification. Presumably the diet of ants or insect grubs made available by the long tongue places little stress on the skull; hammering, with consequent skull reinforcement, appeared well after adaptations of the tongue as a means of extending the scope for its use.

The present study sheds little helpful light on the origins of the Picumninae, except to make clear that this was well after that of the Jynginae, at a time when all the characteristic woodpecker adaptations had already been acquired. It seems most likely that piculets evolved from some early woodpecker stock to exploit the smaller branches and twigs in tropical habitats, but it scarcely seems possible to single out any group of living woodpeckers as near relatives.

Most functional problems concerning the Picidae have been dealt with at length elsewhere. One aspect perhaps deserving further mention here is the extent of kinetic coupling as against independent jaw action. All the Picidae have a postorbital ligament, though weak in *Jynx*, but they are clearly capable of unloading it to permit a high degree of independent jaw action. Photographs of *Jynx* carrying ants to the nest (e.g. Koffan, 1960) show extreme depression of the upper jaw independent of the lower, and the same is shown in lesser degree by some photographs of woodpeckers, e.g. Burton & Coleman, 1976. Obviously the mechanism of this action and its structural basis require much further study.

Phylogeny and affinities with other orders

To conclude this review, evidence from feeding apparatus structure will be gathered together in an attempt to deduce a possible phylogeny for the Coraciiform—Piciform assemblage. The discussion also briefly considers the origins of the Passeriformes and Trogoniformes and other problems highlighted by the proposals of Feduccia (1977, 1979).

1. Phylogeny

The major division indicated by this study is one between the 'typical Piciformes' (Capitoniidae, Indicatoridae, Ramphastidae and Picidae), and the rest (excluding the Bucerotidae, Upupidae and Phoeniculidae, whose position is discussed later). Features in which the two lines differ are numerous and generally consistent, including such major items as the

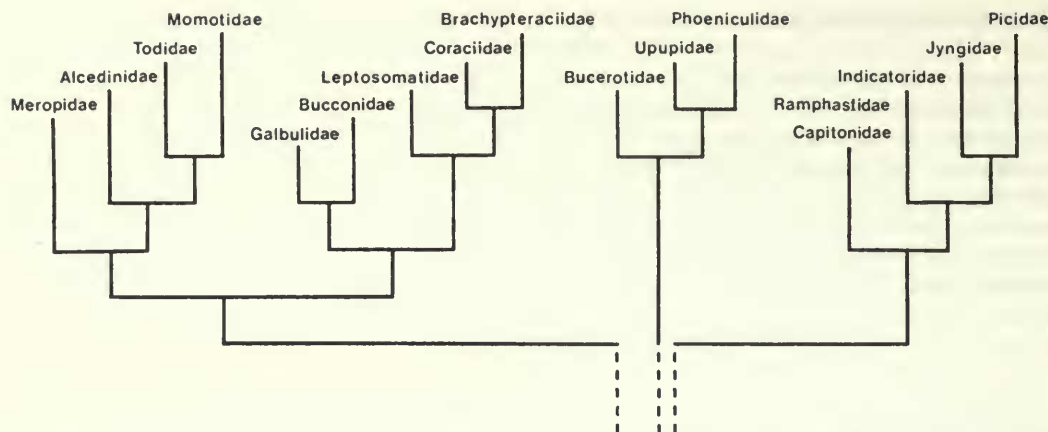


Fig. 32 A possible phylogeny of Coraciiform/Piciform families, as indicated by the features studied here.

structure and siting of *M. pseudotemporalis superficialis*, form and proportion of the hyoid skeleton, structure of *M. hypoglossus obliquus* and origin of *M. tracheohyoideus*. Such differences are fundamental enough to indicate that the two lines have had a long evolutionary separation.

Within the typical Piciformes, the shared characters are predominantly derived ones, and most of them seem unlikely to have arisen more than once. Among the remaining families, the situation is less clear. Those which have been grouped here as 'typical Coraciiformes' share a number of supposedly derived features, such as the invariably desmognathous palate, structure of *M. adductor externus* and *M. pseudotemporalis superficialis*, origin of *M. branchiomandibularis* and *M. tracheohyoideus*, and largely cartilaginous entoglossum. However, the characters linking them are in some cases less consistent than in the typical Piciformes, and the possibility of some being derived more than once appears stronger. To this group of six families it is necessary to add two more—the Galbulidae and Bucconidae (Galbuloidea). They differ radically from the Piciformes, but agree with the Coraciiformes, in almost all the features which this study has shown to be important. Their closest affinities seem to be with the Coraciidae and Leptosomatidae, and indeed this set of four families (Coraciidae, Leptosomatidae, Bucconidae, Galbulidae) appears from the present study to be a clearer natural group than the remaining Coraciiformes (Alcedinidae, Todidae, Momotidae, Meropidae) though the latter are linked by a derived condition of the stapes (Feduccia 1977, 1979). Significant features of feeding apparatus structure shared by them include the long and stout postorbital process, quadrate with very deep medial condyle and broad orbital process, modification of *M. serpihyoideus*, and in all but *Leptosomus*, loss of *M. stylohyoideus*. In the phylogeny, I have consequently grouped them together as a branch diverging early from the main Coraciiform stem.

The remaining three families—the Upupidae, Phoeniculidae and Bucerotidae—also constitute a well defined natural group, sharing such features as a 'retractor palatini' slip of *M. pterygoideus*, anomalous condition of *M. pterygoideus dorsalis*, retroarticular process, and reduced hyoid with characteristic hour-glass shaped basihyal. Traditionally, they have long been linked with the Coraciiformes, but on the basis of features analysed here, they appear to occupy an almost exactly midway position between Coraciiform and Piciform stems. Clearly their separation took place early, but there are indications that they had moved some way along the Piciform pathway when this occurred. Persuasive evidence for this view is provided by the structure of *M. hypoglossus obliquus*, already well modified towards the condition which reaches an extreme in the Picidae. The form and siting of *M. pseudotemporalis superficialis* is also Piciform rather than Coraciiform. *M. tracheohyoideus* originates

as in the Coraciiform families in the Upupidae and Phoeniculidae, but the existence of an intermediate condition in the Bucerotidae suggests that it may have arrived at this stage independently.

To summarize, then, two main branches are visualized in the phylogeny of this assemblage of families. One, leading to the four families of typical Piciformes, branched at an early stage, giving rise to the Upupidae, Phoeniculidae and Bucerotidae. The other, consisting of the 'typical Coraciiformes', has two branches. One includes the Galbuloidea, together with the Coraciidae, Brachypteraciinae (=Brachypteraciidae) and Leptosomatidae; the other embraces the four diverse remaining families, of which the Todidae and Momotidae are perhaps most closely linked. This phylogeny is depicted in Fig. 26.

2. Morphology of the stapes

Feduccia (1977) produced evidence based on the morphology of the bony stapes which seemed to indicate a diphyletic origin for the Passeriformes, the sub-oscine families seeming to show an affinity with some Coraciiformes (Alcedinidae, Todidae, Momotidae and Meropidae). Further evidence (Feduccia, 1979) compelled him to return to the traditional view that the Passeriformes are a monophyletic group, but his findings could still be interpreted to suggest that the ancestors of the Passeriformes had some affinity with the Coraciiformes.

More interestingly, his 'Alcediniformes', sharing a derived stapedial morphology are equivalent to the suborder Alcedines in the classification proposed here. This clearly reinforces the conclusions of the present study, but at the same time raises a further problem, since the Trogoniformes exhibit the same condition. This small and morphologically uniform group have generally been regarded as a distinct order of uncertain affinities. Feduccia (1977) proposes that they branched off from the same stock as the 'Alcediniformes' (=Alcedines) after these had diverged from the 'Coraciiformes'. I shall shortly undertake detailed study of the trogon feeding apparatus in the hope of clarifying their position, but for the present, a few points perhaps deserve comment.

Firstly, since the Trogoniformes retain well developed basipterygoid processes, these must have been lost independently in Alcediniform and Coraciiform lines; however they have undoubtedly been lost independently by many other bird families, so this factor is clearly no obstacle. Second, and more interestingly, an initial examination of Trogon (*Harpactes*) jaw musculature has revealed that *M. pseudotemporalis superficialis* is represented by two virtually separate muscles lying side by side. In structure and siting, the medial part corresponds remarkably closely with the deeper, medial *M. pseud. superf.* of the Piciformes, while the lateral one corresponds with the more lateral and superficial muscle of the typical Coraciiformes. The presence of both at once appears to be the ancestral condition in an almost idealized form. If Feduccia's phylogeny is correct, then here again, the same derived condition—loss of the medial muscle—has arisen independently in both 'Alcediniformes' and 'Coraciiformes'. Thirdly, Trogons lack any trace of desmognathism; consequently, this condition too, must have arisen independently in 'Alcediniformes' and 'Coraciiformes'. A final point concerns the 'retractor palatini' slip of *M. pterygoideus*—a slip from the muscle attached to the basitemporal plate. Among the families studied in this investigation, this feature is found only in the Bucerotidae, Upupidae and Phoeniculidae. However, a 'retractor palatini' is also found in Trogons (Burton, 1974), as in many passerines, but it appears to be of different morphological origin; it is therefore probably of little relevance as regards their phylogenetic placing.

Finally, some comment on the hornbills, hoopoes and wood hoopoes. Feduccia finds that the latter two families share a unique 'anvil' modification of the stapes, whereas the hornbills retain the primitive condition. This is consistent with the findings of the present study inasmuch as the hoopoes and wood hoopoes are shown to be particularly closely related, but I am reluctant to follow him in placing them in a separate order from the hornbills. This investigation has added to the already strong evidence that the three families constitute a distinct natural group, and the classification should reflect this, as in the scheme which follows.

3. Classification

A suggested classification of the Coraciiform and Piciform families is given below; it is based solely on the results of this study, as expressed in the postulated phylogeny depicted in Fig. 26. Ground rollers have been elevated to family status following Cracraft (1971) and wry-necks are given family status for reasons explained earlier in this systematic review. The Capitonidae and Ramphastidae are retained as separate families, though it may be noted that in a strictly cladistic system, their relationship as viewed here (pp. 433–4) should be expressed by merging them as a single family. (See, e.g. Cracraft, 1974). Only extant groups are included in this classification, but hopefully it may eventually prove possible to include fossil discoveries (e.g. Brodkorb, 1976, Feduccia & Martin, 1976, Olson, 1976) within a similar framework.

It would of course be gratifying if future studies of these families from other aspects produce similar results to those presented here, but doubtless some inconsistencies will occur. Where this is the case, I can only hope that the findings of this study have been presented clearly enough to make reinterpretation or reworking feasible.

The proposed classification, then, is as follows:

Order CORACIIFORMES

Suborder ALCEDINES

- Family Meropidae, bee-eaters
- Family Alcedinidae, kingfishers
- Family Todidae, todies
- Family Momotidae, motmots

Suborder CORACII

- Superfamily Galbuloidea
 - Family Galbulidae, jacamars
 - Family Bucconidae, puffbirds
- Superfamily Coracoidea
 - Family Leptosomatidae, cuckoo-rollers
 - Family Coraciidae, rollers
 - Family Brachypteraciidae, ground-rollers

Order UPUPIFORMES

- Superfamily Bucerotidea
 - Family Bucerotidae, hornbills
- Superfamily Upupoidea
 - Family Upupidae, hoopoes
 - Family Phoeniculidae, wood-hoopoes

Order PICIFORMES

- Family Capitonidae, barbets
- Family Ramphastidae, toucans
- Family Indicatoridae, honeyguides
- Family Jynidae, wrynecks
- Family Picidae, woodpeckers

Acknowledgements

No anatomical study can take place without specimens. At the onset of this project, although the collections of the British Museum (Natural History) could provide a large part of the requirements, various crucial species or groups still remained unrepresented. Most of these gaps have now been filled, partly by direct collecting, and partly by gifts, exchanges or loans. Outstanding among the gifts are the valuable

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References

- Allen, A. A. & Kellogg, P. P. 1937. Recent observations on the Ivory-billed Woodpecker. *Auk* **54**: 164-184.
- Appert, O. 1968a. Neues zur Lebensweise und Verbreitung des Kurols, *Leptosomus discolor* (Hermann). *J. Orn., Lpz.* **109**: 116-126.
- Appert, O. (1968b). Zur Brutbiologie der Erdracke *Uratelornis chimaera* Rothschild. *J. Orn., Lpz.* **109**: 264-275.
- Bannerman, D. A. 1951. *The Birds of Tropical West Africa*. Vol. 8. London: Crown Agents for the Colonies.
- Barnikol, A. 1952. Korrelationen in der Ausgestaltung der Schädelform bei Vögeln. *Morph. Jb.* **92**: 373-414.
- Baumel, J. J., King, A. S., Lucas, A. M., Breazile J. & Evans, H. E., Eds. 1979. *Nomina Anatomica Avium*. London: Academic Press.
- Beddard, F. E. 1898. *The structure and classification of birds*. London: Longmans, Green.
- Beecher, W. J. 1951. Adaptations for food-getting in the American Blackbirds. *Auk* **68**: 411-440.
- 1953a. A phylogeny of the Oscines. *Auk* **70**: 270-333.
- 1953b. Feeding adaptations and systematics in the avian order Piciformes. *J. Wash. Acad. Sci.* **43**: 293-299.
- 1962. The bio-mechanics of the bird skull. *Bull. Chicago Acad. Sci.* **11**: 10-33.
- Benson, C. W. 1960. The birds of the Comoro Islands: results of the British Ornithologists' Union Centenary Expedition, 1958. *Ibis* **103b**: 5-106.
- Blandamer, J. S. & Burton, P. J. K. 1979. Anatomical specimens of birds in the collections of the British Museum (Natural History). *Bull. Br. Mus. nat. Hist. (Zool.)* **34**: 125-180.
- Boas, J. E. V. 1929. Biologisch-anatomische Studien über den Hals der Vogel. *K. dansk. Vidensk. Selsk. Skr.* (Naturvidenskab. Math. Afdel.) Ser. 9, **1**: 102-222.

- Bock, W. J. 1960a. Secondary articulation of the avian mandible. *Auk* 77: 19–55.
- 1960b. The palatine process of the premaxilla in the Passeres. *Bull. Mus. comp. Zool., Harv.* 122: 361–488.
- 1964. Kinetics of the avian skull. *J. Morph.* 114: 1–42.
- 1966. An approach to the functional analysis of bill shape. *Auk* 83: 10–51.
- 1972. Morphology of the tongue apparatus of *Ciridops anna* (Drepanididae). *Ibis* 114: 61–78.
- Bock, W. J. & Morony, J. 1972. Snap-closing jaw ligaments in flycatchers. *Am. Zool.* 12: 722.
- Brodkorb, P. 1976. Discovery of a Cretaceous Bird, Apparently Ancestral to the Orders Coraciiformes and Piciformes (Aves: Carinatae). *Smithson. Contr. Paleobiol.* 27: 67–73.
- Brown, L. in Gooders, J. (Ed.) 1969–71. Vol. 5, *Common Scimitar-bill*: pp. 1563–1564.
- Bühler, P. 1970. Schädelmorphologie und Kiefermechanik der Caprimulgidae (Aves). *Z. Morph. Tiere* 66: 337–399.
- 1981. Functional anatomy of the avian jaw apparatus. In King, A. S. & McLelland, J. (Eds.), *Form and Function in Birds*, Vol. 2: 439–468. London: Academic Press.
- Burt, W. H. 1930. Adaptive modifications in the Woodpeckers. *Univ. Calif. Publ. Zool.* 32: 455–524.
- Burton, P. J. K. 1971. Some observations on the splenius capitis muscle of birds. *Ibis* 113: 19–28.
- 1972. Two bird specimens showing abnormalities of the quadrate. *Auk* 89: 882–885.
- 1974a. *Feeding and the feeding apparatus in waders: a study of anatomy and adaptations in the Charadrii*. London: British Museum (Natural History).
- 1974b. Anatomy of head and neck in the Huia (*Heteralocha acutirostris*) with comparative notes on other Callaeidae. *Bull. Br. Mus. nat. Hist. (Zool.)* 27: 1–48.
- 1974c. Jaw and tongue features in Psittaciformes and other orders with special reference to the anatomy of the Tooth-billed pigeon (*Didunculus strigirostris*). *J. Zool., Lond.* 174: 255–276.
- 1977a. Feeding behaviour in the Paradise Jacamar and the Swallow-wing. *Living Bird* 15: 223–238.
- 1977b. Lower jaw action during prey capture by pelicans. *Auk* 94: 785–786.
- 1978. The basisphenoid notch of kingfishers. *Bull. Br. Orn. Cl.* 98: 68–74.
- 1979. Notes on some waders and kingfishers in Sarawak. *Sarawak Mus. J., New Series* 26 (1978): 195–204.
- 1981. Studies of Functional Anatomy in Birds Utilising Museum Specimens. *Int. orn. Congr.* XVII: 190–194.
- Burton, R. & Coleman, B. 1976. *The wondrous world of birds*. New Malden, Surrey: Colour Library International.
- Cracraft, J. 1968. The lacrimal-ectethmoid bone complex in birds: a single character analysis. *Am. Midl. Nat.* 80: 316–359.
- 1971. The relationships and evolution of the rollers: families Coraciidae, Brachypteraciidae, and Leptosomatidae. *Auk* 88: 723–752.
- 1972. The relationships of the higher taxa of birds: problems in phylogenetic reasoning. *Condor* 74: 379–392.
- 1974. Phylogenetic models and classification. *Syst. Zool.* 23: 71–90.
- Cunningham, R. O. (1870). Notes on some points in the anatomy of three Kingfishers (*Ceryle stellata*, *Dacelo gigas* and *Alcedo ispida*). *Proc. zool. Soc. Lond.* 1870: 280–283.
- Douthwaite, R. J. 1976. Fishing techniques and foods of the Pied Kingfisher on Lake Victoria in Uganda. *Ostrich* 47: 153–160.
- Eastman, R. 1969. *The Kingfisher*. London: Collins.
- Engels, W. L. 1938. Tongue musculature of passerine birds. *Auk* 55: 642–650.
- England, M. D. 1973a. Breeding the red-fronted barbet (*Tricholaema diadematum*). *Avicult. Mag.* 79: 9–13.
- 1973b. Breeding the red and yellow barbet (*Trachyphonus erythrocephalus*). *Avicult. Mag.* 79: 194–196.
- 1975. Breeding the red-headed barbet *Eubucco bourcierii*. *Avicult. Mag.* 81: 121–130.
- 1976. Breeding the Double-toothed Barbet *Lybius bidentatus*. *Avicult. Mag.* 82: 191–193.
- 1977. Breeding the Spotted-flanked Barbet *Tricholaema lacrymosum*. *Avicult. Mag.* 83: 1–2.
- Feduccia, A. 1977. A model for the evolution of perching birds. *Syst. Zool.* 26: 19–31.
- 1979. Comments on the phylogeny of perching birds. *Proc. biol. Soc. Wash.* 92: 689–696.
- 1980. *The age of birds*. Cambridge, Mass.: Harvard University Press.
- Feduccia, A. & Martin, L. D. 1976. The Eocene zygodactyl birds of North America (Aves: Piciformes). *Smithson. Contr. Paleobiol.* 27: 101–110.

- Fiedler, W. 1951. Beiträge zur Morphologie der Kiefermuskulatur der Oscines. *Zool. Jb. (Anat.)* **71**: 236–288.
- Fisher, H. I. 1955. Some aspects of the kinetics in the jaws of birds. *Wilson Bull.* **67**: 175–188.
- Fogden, M. P. L. in Gooders, J. (Ed.) 1969–71. Vol. 5, *Black Hornbill*: pp. 1569–1570.
- Forbes-Watson, A. D. 1967. Observations at a nest of the cuckoo-roller *Leptosomus discolor*. *Ibis* **109**: 425–430.
- Friedmann, H. 1955. The Honey-guides. *Bull. U.S. natn. Mus.* **208**: vii+292 pp.
- Fry, C. H. 1969. The recognition and treatment of venomous and non-venomous insects by small bee-eaters. *Ibis* **111**: 23–29.
- 1970a. Ecological Distribution of Birds in North-Eastern Mato Grosso State, Brazil. *Anais Acad. bras. Cienc.* **42**: 275–318.
- 1970b. Convergence between jacamars and bee-eaters. *Ibis* **112**: 257–259.
- 1972. The biology of African bee-eaters. *Living Bird* **11**: 75–112.
- 1980. The evolutionary biology of kingfishers (Alcedinidae). *Living Bird* **18**: 113–160.
- Garrod, A. H. 1872. Notes on some cranial peculiarities of the Woodpeckers, *Ibis* **1872**: 357–360.
- Gooders, J. (Ed.) 1969–71. *Birds of the World*. 10 vols. London: IPC Magazines.
- Goodman, D. C. & Fisher, H. J. 1962. *Functional Anatomy of the Feeding Apparatus in Waterfowl (Aves: Anatidae)*. Carbondale, Ill.: Southern Illinois University Press.
- Haffer, J. 1974. Avian speciation in tropical South America with a systematic survey of the Toucans (Ramphastidae) and Jacamars (Galbulidae). *Publs Nuttall orn. Club* **14**: viii+390 pp.
- Hofer, H. 1950. Zur Morphologie der Kiefermuskulatur der Vögel. *Zool. Jb. (Anat.)* **70**: 427–556.
- Hughes, A. F. W. 1934. On the development of the blood vessels in the head of the chick. *Phil. Trans. R. Soc. Ser. B*, **224**: 75–129.
- Huxley, T. H. 1867. On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. *Proc. zool. Soc. Lond.* : 415–472.
- Hyatt, K. H. in Gooders, J. (Ed.) 1969–71. Vol. 5, *Coppersmith Barbet*: pp. 1589–1590.
- Jenni, L. 1981. Das Skelettmuskelsystem des Halses von Buntspecht und Mittelspecht *Dendrocopos major* und *medius*. *J. Orn.* **122**: 37–63.
- Johnson, R. A. 1954. The behaviour of birds attending army ant raids on Barro Colorado Island, Panama Canal Zone. *Proc. Linn. Soc. N.Y.* **63–65**: 41–70.
- Junge, C.-J. & Lütken, E. 1974. The Shy and Spectacular Kingfisher. *Natn. geogr. Mag.* **146**: 412–419.
- Keast, A. in Gooders, J. (Ed.) 1969–71. Vol. 5, *Laughing Kookaburra*: pp. 1513–1514.
- Kemp, A. C. 1976. A Study of the Ecology Behaviour and Systematics of *Tockus* Hornbills (Aves: Bucerotidae). *Transv. Mus. Mem.* No. 20: 125 pp.
- Kepler, A. K. 1977. Comparative study of todies (Todidae); with emphasis on the Puerto Rican today, *Todus mexicanus*. *Publs Nuttall orn. Club* No. 16: xiii+190 pp.
- Koffan, K. 1960. *Birds in Camera*. London: Barrie & Rockliff.
- Kripp, D. V. 1935. Die mechanische Analyse der Schnabelkrümmung und ihre Bedeutung für die Anpassungsforschung. *Morph. Jb.* **76**: 448–494.
- Lakjer, T. 1926. *Studien über die trigeminus-versorgte Kaumuskulatur der Sauropsiden*. Copenhagen: Reitzel.
- Lebedinsky, N. G. 1921. Zur Syndesmologie der Vögel; *Anat. Anz.* **54**: 8–15.
- Leiber, A. 1907a. Vergleichende Anatomie der Spechtzunge. *Zoologica, Stuttg.* **51**: vi+79 pp.
- 1907b. Bau und Funktion der Spechtzunge in ihren gegenseitigen Beziehungen. *Z. EntwLehre, Stuttg.* **1**: 32–53.
- Lorenz, K. 1949. Über die Beziehungen zwischen Kopform und Zirkelbewegung bei Sturniden und Icteriden. In Mayr, E. & Schuz, E. (Eds.) *Ornithologie als biologische Wissenschaft*: pp. 153–157. Heidelberg: Carl Winter Universitätsverlag.
- Lowe, P. R. 1946. On the systematic position of the woodpeckers (Pici), honeyguides (*Indicator*), hoopoes and others. *Ibis* **88**: 103–127.
- 1948. What are the Coraciiformes? *Ibis* **90**: 572–582.
- Maclean, G. L. 1971. Sharp-billed Honeyguide Parasitising Neddicky in Natal. *Ostrich* **42**: 75–77.
- Manger Cats-Kuenen, C. S. W. 1961. Casque and bill of *Rhinoplax vigil* (Forst.) in connection with the architecture of the skull. *Verh. K. ned. Akad. Wet.* **53**: 1–51.
- Marinelli, W. 1928. Über den Schädel der Schnepfe. *Palaeobiologica* **1**: 136–160.
- Massny, H. 1977. Beobachtungen im Brutrevier des Eisvogels. *Falke* **24**: 304–307.
- Maurer, D. R. & Raikow, R. J. (in press). Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Ann. Carneg. Mus.*

- Miller, A. H. 1947. The tropical avifauna of the upper Magdalena Valley, Columbia. *Auk* **64**: 351-381.
- Möller, W. 1930. Über die Schnabel-und Zungenmechanik blütenbesuchender Vogel. I. *Biologia gen.* **6**: 651-726.
- Morony, J. J., Jr., Bock, W. J. & Farrand, J., Jr. 1975. *Reference list of Birds of the World*. New York: American Museum of Natural History.
- Murie, J. 1872a. On the motmots and their affinities. *Ibis* **14**: 383-412.
- 1872b. On the skeleton of *Todus*, with remarks as to its allies. *Proc. zool. Soc. Lond.* **1872**: 664-680.
- 1873. On the Upupidae and their relationships. *Ibis* **15**: 181-211.
- Olson, S. L. 1976. Oligocene fossils bearing on the origins of the Todidae and the Momotidae (Aves: Coraciiformes). *Smithson. Contr. Paleobiol.* **27**: 111-119.
- Palmgren, P. 1949. Zur biologischen Anatomie der Halsmuskulatur der Singvögel. In *Ornithologie als biologische Wissenschaft*, pp. 192-203. Heidelberg: Carl Winter Universitätsverlag.
- Parker, W. K. 1875. On the morphology of the skull in the woodpeckers (Picidae) and wrynecks (Yungidae). *Trans. Linn. Soc. Lond.*, 2nd Ser., Zool., **1**: 1-22.
- Peters, J. L. 1945. Check-list of birds of the world. Vol. 5. Cambridge, Mass: Harvard University Press.
- 1948. *Idem* Vol. 6.
- Rand, A. L. 1964. Cuckoo-roller. In Thomson, A. L. (Ed.) 'A New Dictionary of Birds'. London: British Ornithologists' Union.
- Richards, L. P. & Bock, W. J. 1973. Functional anatomy and adaptive evolution of the feeding apparatus in the Hawaiian honeycreeper genus *Loxops* (Drepanididae). *Orn. Monogr.* **15**: x+173 pp.
- Robinson, H. C. 1928. *The Birds of the Malay Peninsula*. Vol. 2. *The Birds of the Hill Stations*. London: Witherby.
- Shufeldt, R. W. 1884. Osteology of *Ceryle alcyon*. *J. Ant. Physiol. Lond.* **18**: 279-294.
- 1890a. Contributions to the comparative osteology of Arctic and sub-Arctic waterbirds. Part VII. *J. Ant. Physiol. Lond.* **24**: 343-366.
- 1890b. *Idem*, Part VIII. *Ibid.* **25**: 60-77.
- 1891. On the question of saurognathism of the Pici, and other osteological notes upon that group. *Proc. zool. Soc. Lond.* **1891**: 122-129.
- Sibley, C. G. & Ahlquist, J. E. 1972. A Comparative Study of the Egg White Proteins of Non-Passerine Birds. *Bull. Peabody Mus. nat. Hist.* **39**: vi+276 pp.
- Sielmann, H. 1961. *My year with the woodpeckers*. London: Barrie and Rockliff.
- Simpson, S. F. & Cracraft, J. 1981. The phylogenetic relationships of the Piciformes (class Aves). *Auk* **98**: 481-494.
- Skead, C. J. 1950. A study of the African Hoopoe. *Ibis* **92**: 434-463.
- Skutch, A. F. 1937. Life-history of the Black-chinned Jacamar. *Auk* **54**: 135-146.
- 1944. The life-history of the Prong-billed Barbet. *Auk* **61**: 61-88.
- 1948. Life history notes on Puff-birds. *Wilson Bull.* **60**: 81-97.
- 1958. Life history of the White-whiskered Soft-wing *Malacoptila panamensis*. *Ibis* **100**: 209-231.
- 1963. Life history of the Rufous-tailed jacamar *Galbula ruficauda* in Costa Rica. *Ibis* **105**: 354-368.
- 1964. Life history of the Blue-diademed Motmot *Momotus momota*. *Ibis* **106**: 321-332.
- 1967. Life histories of Central American Highland Birds. *Publs Nuttall orn. Club* **7**: vi+213 pp.
- 1969. Life histories of Central American Birds III. *Pacif. Cst. Avifauna* **35**: 580 pp.
- 1971. Life history of the Broad-billed Motmot with notes on the Rufous Motmot. *Wilson Bull.* **83**: 74-94.
- 1972. Studies of Tropical American Birds. *Publs Nuttall orn. Club* **10**: vi+228 pp.
- Smythies, B. E. 1953. *Birds of Burma*. Edinburgh & London: Oliver & Boyd.
- 1960. *The Birds of Borneo*. Edinburgh: Oliver & Boyd.
- Spring L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. *Condor* **67**: 457-488.
- Starck, D. 1940. Beobachtungen an der Trigemimusmuskulatur der Nashornvögel. *Morph. Jb.* **84**: 585-623.
- Starck, D. & Barnikol, A. 1954. Beiträge zur Morphologie der Trigemimus-muskulatur der Vögel. *Morph. Jb.* **94**: 1-64.
- Steinbacher, J. 1934. Untersuchungen über den Zungenapparat indischer Spechte. *J. Orn.* **8**: 399-408.
- 1935. Ueber den Zungenapparat sudafrikanischer Spechte. *Orn. Mber.* **43**: 85-89.

- 1937. Anatomische Untersuchungen über die systematische Stellung der Galbulidae und Bucconidae. *Arch. Naturgesch.*, N.S. **6**: 417–515.
- 1941. Weitere Untersuchungen über den Zungenapparat afrikanischer Spechte. *Orn. Mber.* **49**: 16–137.
- 1955. Zur Morphologie und Anatomie des Zungenapparates brasilianischer Spechte. *Senckenburg. biol.* **36**: 1–8.
- 1957. Über den Zungenapparat einiger neotropische spechte. *Senckenburg. biol.* **38**: 259–270.
- Strauch, J. G. Jr.** 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Trans. zool. Soc. Lond.* **34**: 263–345.
- Swierczewski, E. V. & Raikow, R. J.** 1981. Hind limb morphology, phylogeny, and classification of the Piciformes. *Auk* **98**: 466–480.
- Tanner, J. T.** 1942. *The Ivory-billed Woodpecker*. New York: National Audubon Society.
- Thiollay, J. M.** 1971. Les guepiers et rolliers d'une zone de contact savane-forêt en Côte d'Ivoire. *L'Oiseau* **41**: 148–162.
- Thomson, A. L. (Ed.)** 1964. *A new Dictionary of Birds*. London: British Ornithologists' Union.
- Verheyen, R.** 1955a. Contribution à la systématique des Piciformes basée sur l'anatomie comparée. *Bull. Inst. r. Sci. nat. Belg.* **31** (50–51): 43 pp.
- Verheyen, R.** 1955b. Analyse du potentiel morphologique et considérations sur la systématique des Coraciiformes (Wetmore 1934). *Bull. Inst. r. Sci. nat. Belg.* **31** (92–94): 51 pp.
- Wetmore, A.** 1968. The birds of the Republic of Panama. Part 2. *Smithson. misc. Collns* **150**: v+605 pp.
- Yudin, K. A.** 1961. (On the mechanism of the jaw in the Charadriiformes, Procellariiformes and some other birds). *Trudy zool. Inst. Leningr.* **29**: 257–302. (In Russian).
- 1965. (The phylogeny and classification of the Charadriiformes). *Fauna SSSR*, Nov. Ser. **91**: 26P pp. (In Russian).
- Zusi, R. L.** 1959. The function of the depressor mandibulae muscle in certain passerine birds. *Auk*, **76**: 537–539.
- 1962. Structural adaptations of the head and neck in the black skimmer *Rynchops nigra* Linnaeus. *Publ. Nutt. orn. Club* **3**: vii+101 pp.
- 1967. The role of the Depressor Mandibulae Muscle in Kinesis of the Avian Skull. *Proc. U.S. natn. Mus.* **123** (3607): 28 pp.
- Zusi, R. L. & Marshall, J. T.** 1970. A comparison of Asiatic and North American sapsuckers. *Nat. Hist. Bull. Siam. Soc.* **23**: 393–407.
- Zusi, R. L. & Storer, R. W.** 1969. Osteology and myology of the head and neck of the Pied-billed Grebe (*Podilymbus*). *Mus. Zool. Univ. Michigan* **139**: 1–49.
- Zweers, G. A.** 1974. Structure, movement and myography of the feeding apparatus of the Mallard (*Anas platyrhynchos* L.). A Study of functional Anatomy. *Neth. J. Zool.* **24**: 323–467.
- 1981. Experimental Functional Analysis and Formulation of Causal Models. *Int. orn. Congr.* **XVII**: 195–201.